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A REVIEW OF THE NOTOSTRACA

ALAN R. LONGHURST

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
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A REVIEW OF THE NOTOSTRACA

BY

ALAN R. LONGHURST

(Bedford College, University of London)

Pp. 1–57 ; 16 *Text-figures*

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
ZOOLOGY Vol. 3 No. 1
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THE BRITISH MUSEUM

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A REVIEW OF THE NOTOSTRACA

By ALAN R. LONGHURST

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SYNOPSIS

This paper reviews the known species of Notostraca on the basis of a large collection of museum material and on information from the literature. The genus *Triops* is reduced to four, and the genus *Lepidurus* to five species.

The species of *Triops* are separated on the armature of the telson and on the presence or absence of a second maxilla; in each species there is considerable variation in the segment number, and in the many structures whose variation is shown to be correlated with this number.

The segment number is more constant in *Lepidurus* and fewer structures are correlated with its variation; this genus appears to fall into two groups, as Linder (1952) suggested, on the basis of the segment number. A new species of *Lepidurus* is described from Russia.

In addition to the analysis of the validity of the systematic characters from work on preserved specimens, evidence derived from the growth and development of living animals, their cytology, their reproduction and their protein specificity are also considered.

INTRODUCTION

THE Notostraca are an order of Euphyllopod Crustacea with shield-shaped carapace, consisting of a single family with two genera; *Triops* (= *Apus*) and *Lepidurus*. They usually occur in temporary pools of fresh or brackish water, being most common in the drier parts of the world where the surface water is often of a temporary nature.

Their adaptation to a temporary habitat has enabled their drought-resistant eggs to become efficient agents of passive dispersal, so that populations occur on remote oceanic islands and are apparently found wherever there are suitable pools.

These animals are of interest to the general zoologist not only on account of their primitive nature, but also because they exemplify an animal in evolutionary stagnation. The family has been in existence since the Permian, and forms from the Triassic are almost indistinguishable from one of the extant species.

Individually Notostraca are notoriously variable and differences in the armature of spines on the exoskeleton, or in bodily proportions, can be found in any pair of animals, even those from the same pool. This, together with the lack of conspicuous morphological discontinuities within the genera, makes the group a " difficult " one systematically, and has resulted in the excessive number of descriptions—of specimens rather than species—with which the synonymies are now burdened.

There have been several revisions of the group as a whole, but none later than that of Simon (1886) who revised the species then known to him. Barnard (1929), Linder (1952) and Tiwari (1952) have reviewed regional material from South Africa, North America and India respectively, and have tended towards a reduction in the number of species recognized, placing many names into the synonymies. This trend has been general in recent years but has by no means prevented the description of new species on inadequate grounds.

Because of their interest from a systematic and evolutionary point of view, their geological age, their passive distribution, and their restricted habitat, it was evident that a review of the Notostraca based on a comprehensive collection of preserved specimens and on a study of the growth and cytology of living animals was desirable ; one of the points of agreement between recent authors on the group has been the need for such a revision.

MATERIALS

The preserved specimens of Notostraca on which this revision is based consist of more than 200 samples, of which about 160 are of *Triops* ; the number of specimens in each sample varies and the majority contain less than 10 individuals, although a few have more than 100 specimens from the same locality.

The bulk of this material is formed by the collections of the British Museum and of the Muséum Nationale d'Histoire Naturelle, Paris ; the remainder was on loan from the U.S. National Museum in Washington, the Western Australian Museum in Perth, the Zoological Survey of India in Calcutta, and the Museo de Ciencias Naturalis in Madrid. A few samples of preserved Notostraca were sent to me by private individuals.

The living material was reared in the laboratory from eggs in dried mud sent to me from phyllopod pools all over the world. Many contained no viable eggs, but successful hatchings were obtained from the following samples (collector's name in parentheses) : *Triops cancriformis*—Sweden (P. Ardö), England (A. R. Longhurst), France (D. Schachter), Italy (H. M. Fox) ; *T. granarius*—Johannesburg (van der Horst), Grahamstown (J. Omer-Cooper), Iraq (A. James) ; *T. longicaudatus*—California (L. E. Rosenberg) ; *T. australiensis*—Ayers Rock (I. Thomas, F. McNeill, A. L. Rose), Kalgoorlie, Ballodonia (A. R. Main) ; *Lepidurus arcticus*—Iceland (H. Moore) ; *L. apus*—New Zealand (A. Lysaght, E. Percival).

Living cultures of Notostraca were successfully maintained in the laboratory under reasonably standard conditions. Larvae hatched readily from the mud samples when these were placed in a tank of clean water (either filtered pond water or dechlorinated tap water) which were maintained at about 20° C, air being bubbled through the water. If an excess of mud was put in a tank bacterial growth was very rapid and the culture was soon lost ; about $\frac{1}{4}$ in. on the bottom of a 24 in. by 12 in. tank proved suitable.

The larvae fed at first on the organic content of the mud and if the production of diatoms and Protozoa was poor in the culture in its early stages an addition of cultured *Chlorella* was very beneficial to the growth of the larvae. From about 1 cm. in length growth was more rapid if additional food was provided ; this consisted of chopped annelid worms (*Tubifex*), live *Daphnia* and an artificial food. This last was made up from equal parts by weight of dried *Daphnia*, grass-flour, and Bemax (a proprietary cereal food) ground together into a fine powder and suspended in calcium alginate jelly. This was then chopped and formed a satisfactory basic diet for adult Notostraca.

The eggs laid in the cultures were hatched by allowing the mud which contained them to dry out slowly ; on re-wetting, a high proportion of them hatched successfully. A more rapid and effective way of maintaining a culture was to collect the eggs as they were laid and to transfer them to a beaker of clean tap water with an addition of 30–50% of glass-distilled water ; this low osmotic pressure medium induced hatching after 12–14 days without prior drying, in the same manner as Hall (1953) has described for the eggs of *Chirocephalus diaphanus*. The larvae live for only a few moments in this water however, and must be removed from it at once.

I am most grateful to those who sent me samples of mud (including those from which I was unable to hatch Notostraca and which are not listed above) and to those people who collected and sent preserved specimens. My thanks are also due to the Authorities of the Museums listed above who lent me material, and especially to the Trustees and Staff of the British Museum (Natural History) and the Muséum Nationale d'Histoire Naturelle, who generously gave me facilities for examining their collections. I am particularly indebted to Dr. J. P. Harding of the British Museum who has given me invaluable help during the whole time that I have been studying the group.

The work on living animals was done in the Zoology Department of Bedford College, University of London under the supervision of Professor H. Munro Fox, to whom I am grateful for much assistance.

A maintenance grant from the Department of Scientific and Industrial Research, and a special grant from the Central Research Fund of the University of London were received during the work.

Abbreviations.—In the text the museums listed above are referred to by the following sets of initials :

BMNH	London.
USNM	Washington.
MNHNP	Paris.
WAM	Perth.
ZSI	Calcutta.

SYSTEMATIC CHARACTERS

The systematics of the Notostraca have been based almost entirely on characters of the setae and spines which comprise the armature of the exoskeleton, and on the proportions of various parts of the body—the endites, the furca and the carapace. The validity of these characters was discussed in Barnard's revision of the South African forms (Barnard, 1929). More recently, the review by Linder (1952) further explored this field and has added several characters which prove useful in separating species. The description of new species from European and North African material by Ghigi (1921) initiated a discussion on the validity of the characters which he used, to which Colosi (1922), Gurney (1923), and Gauthier (1933, 1934) contributed.

Before any character can properly be used in systematics it is essential that its variation in adult individuals be known, and that its development or change during the growth of a single individual should have been studied ; in the present review the validity of as many as possible of the systematic characters has been studied and several new ones are proposed.

Previous authors have been concerned almost without exception with the variation of characters in samples of adult individuals, and it has been possible to extract much useful information about this from the literature, which has been combined with that obtained from the study of the museum material.

A pure line of individuals from a hermaphrodite *Triops cancriformis* from Britain was raised under standard conditions ; a large batch of eggs was collected from the parent, hatched, and reared at first in a single large culture dish, later being transferred to individual dishes, each with the same volume of water and mud ; the dishes standing in a room thermostatically controlled at 20° C (± 1° C). A surplus of the artificial food was always available to the animals. From this culture 25 individuals were preserved and their variation studied ; all these animals were preserved after growth changes had ceased in the characters to be studied.

The change of several characters during growth was studied by Linder (1952) in museum material ; he based his conclusions on specimens which were about to ecdyse, in which both the old and the new exoskeletons could be observed. In the present review living material of all species of *Triops* was studied during growth from larva to adult ; the changes in relative proportions during growth have been examined and the size at which the exoskeletal armature becomes stable determined.

A start has also been made on the effects of environmental factors on morphology, but the experiments have not been very successful. *Triops* is a difficult animal to grow under precisely standardized conditions, for it has not been possible to rear them without a little mud in their dishes even when they are fed artificially. Main (1953) has suggested that so-called specific differences in Australian forms may be due to differences in the salinity of the medium ; I have made attempts to grow *Triops* at salinities near those that Main found in the field, but the animals have rapidly died each time. The temperature at which the animals were reared might be expected to have some effect on their form, and so a pure line of *T. cancriformis* was grown at a temperature (25–28° C) near their lethal point, but these animals showed little difference from those grown at normal temperatures.

Notostraca were grown in the laboratory under very diverse conditions of temperature, food, and vessel size, but all have remained remarkably uniform in their morphology. *Daphnia* under parallel conditions would show very marked morphological changes, and it is probably safe to assume that environmental factors can affect the morphology only after a very considerable number of generations—as salinity affects the form of *Artemia salina* only after several years (Schmankiewitsch, 1875).

The various characters which have been used in systematics are now examined separately.

(1) *Total size*

Samples of adult Notostraca usually contain individuals of very different sizes, and it is difficult to determine whether there is a normal adult size for any species. The growth rates of animals in a batch of *Triops* reared in the laboratory are also very variable (Fox, 1949) as the pure line of *T. cancriformis* showed very clearly; after a few days growth they varied enormously in size; 33 individuals were between 2·0 and 3·5 mm. carapace length, while one was only 1·5 mm., and another 5·0 mm. Spandl (1926) gives growth curves for individual *T. cancriformis*, maintaining that those which grow the fastest become the largest, which is what one would expect if the growth rate depended on the level of nutrition.

The usual adult size for all species seems to be between 15 mm. and 30 mm. in carapace length, the growth curve flattening out somewhere between these two figures.

The total size has occasionally been used as a systematic character.

Bowkiewicz (1923) suggests that giant *Triops* which he saw in Siberia might be a new species; large individuals of other species occur up to 40 mm in carapace length and probably correspond to the giant specimens of Anostraca, which Sellier and Morice (1946) have shown to be cytologically similar to normal individuals in one species (*Chirocephalus diaphanus*).

It is difficult to find a suitable measure of the total size of individuals in order that relative proportions of endites, etc. may be compared during growth in different samples. The total length has been shown to be quite useless in preserved specimens (Barnard, 1929; Sømme, 1934; Linder, 1952) and is difficult to measure in living animals, which have considerable powers of contraction. The measurements made on living animals also indicate that there is some increase in length during an instar. Sømme (1934) showed that the median carapace length is more reliable for it is little affected by the action of the preservative.

It has now been possible to show that the growth of the carapace is isometric and is therefore a valid measurement of size at all ages (p. 11).

Unfortunately, the ratio of carapace length/total length varies between samples and so this measurement is valid only in comparisons within a sample.

Generally, *Lepidurus* spp. tend to be smaller than *Triops* spp. and *Lepidurus arcticus* is usually smaller than the rest, but probably more rarely achieves its maximum size than the non-boreal species.

(2) *Colour*

Living Notostraca are frequently brightly coloured, the colours being due to two main pigments within the body and the brown colour of the exoskeleton.

The internal pigments are haemoglobin, which is present in solution in the blood (Régnard and Blanchard, 1883), and a dark blue-green pigment which occurs in connective tissue in many parts of the body; this pigment is of unknown composition, but is similar in nature to that which occurs in some Ostracods (Fox, 1955).

The concentration of haemoglobin varies inversely with the oxygen tension of the medium in which the animal is living (Fox, 1949), and large animals in poorly aerated conditions may have so dense a concentration that the animal appears to be deep red in colour.

The blue-green pigment appears to be more abundant in *Lepidurus* than in *Triops* and the animal is sometimes deep green in colour (hence *Lepidurus viridis*, Baird). In *Triops* it may be completely absent, though a mid-dorsal patch on the carapace and smaller areas on the bases of the thoracic appendages are generally present. It seems to be more abundant in animals which have grown rapidly and under good conditions, when it forms a dark marbling on the carapace and is well distributed elsewhere. The only living specimens of *T. australiensis* that I have seen have been without this pigment, but this is unlikely to have any significance.

The newly hatched larvae of both genera may be densely coloured with a carotenoid pigment, as Fox (1949) reported for *Triops cancriformis*; in successive generations of the same stock the colour of the larvae is very variable and probably depends on the feeding of the parents; well fed females usually contain eggs which are pink with carotenoid, while in starved specimens they are white.

The egg shells of *Triops* are bright red in colour, for a red haemochromogen is present in them (Fox, 1955); this pigment is secreted by the follicle ducts of the ovary, and is brightest in colour in newly laid eggs, becoming duller after they have been dried.

A bright violet pigment occurs in the egg shell of *Lepidurus arcticus* (H. Moore, personal communication), while other species in this genus have eggs of the same colour as in *Triops*.

(3) *Body-length, segmentation, and number of appendages.*

The carapace of Notostraca is attached only to the head region, and the thorax and abdomen are completely free from it; the post-carapace region is divided into a number of segments or body rings, which have considerable powers of telescoping. The first eleven segments, of which the first is incomplete dorsally, normally each bear one pair of appendages ventrally, and together comprise the thorax.

The number of post-thoracic, or abdominal, segments is variable and the series of appendages is continued along them; a few segments at the posterior end of the abdomen bear no appendages.

Linder (1952) has analysed a great deal of North American material and has to a great extent elucidated the relationships between the number of segments, the number of appendages and the number of apodous segments posteriorly. He concludes that the number of segments and the number of appendages are the results of two quite separate growth processes for a number of reasons: the production of segments and appendages in the larvae proceed at different rates; the boundaries of the appendage bearing segments are not complete ventrally; an aberration in which the segments are spiral instead of annular does not upset the arrangement of the appendages; no correlation can be found between the number of appendages and the segments bearing them; and the appendage series may end anywhere along the length of a segment.

While studying the development of the systematic characters during growth I found that the larvae of *Triops* complete their segmentation by the 5th or 6th instar, but that the series of appendages continue to increase and encroach posteriorly on to fresh segments until the 8th or 9th instar, after which the number of apodous segments remains constant. After this the number of appendages may continue to increase for a few instars but come to occupy no further segments. So after the 9th instar the number of segments and the number which are apodous may be taken as fixed in an individual, so that these could validly be used as characters in animals of more than 3–4 mm. in median carapace length.

The total number of segments varies in *Triops* from 32–44, and in *Lepidurus* from 26–34; these results are based on the museum material combined with information from the literature. Throughout this paper the figures given do *not* include the telson which is considered to be post-segmental, and incomplete segments are included in the count.

The figures for *Triops* show that the variation is continuous throughout its range, and separation into groups on the number of segments would be quite arbitrary; the results for females from all sources illustrates this—

No. of segments .	32	33	34	35	36	37	38	39	40	41	42	43
No. of occurrences .	24	31	19	12	11	17	22	12	13	15	10	7

The bottom row of numbers—the number of occurrences—is obtained by counting the number of samples in which each segment-number occurs; this prevents undue weight being given to large samples, which are not evenly distributed along the range of variation.

The apparent bimodality of these figures is due to the fact that one species—*Triops cancriformis*—has a range of segment variation which covers only a part of that of the other species. This species occurs in Europe and naturally predominates in the collections, thus increasing the number of occurrences at the lower end of the scale. *T. cancriformis* has a variation of 32–35, while the other species probably run from 32–43.

By far the greatest number of *Lepidurus* examined fall within the range of 25–29 segments; I have seen only two samples with more, *L. lynchi* Linder and *L. batesoni* sp. n. This is in accordance with Linder's findings, for he suggested that there might be two groups of species within *Lepidurus* based on the number of segments.

The variation within samples bears out the theory that the number of segments may be of use in the systematics of *Lepidurus* but not of *Triops*; in the pure line of *T. cancriformis* there was a variation of 3 in this character (33–35), and variations of 2, 3, or 4 are usual in samples of preserved specimens. In *Lepidurus*, however, possibly because there are fewer segments, the variation is smaller, rarely being more than 2 in each sample, many samples showing none.

The number of appendages confirms the above grouping of *Lepidurus* ; the shorter bodied group has from 35–48 appendages, the longer from 39–71 ; these figures are based on Linder's data with the addition of counts made on the material I have examined. But in *Triops* I can find no correlation between the number of legs and the number of segments, for high numbers of appendages occur in both short and long bodied specimens, and the converse is also true. In this genus I can find no significance in the numbers of appendages.

The number of apodous segments is a secondary character depending on the interplay of the processes which control appendage and segment formation (Linder, 1952). This is confirmed in my data, most commonly with males and females from the same sample ; the males tending to have a smaller number of appendages, the same number of segments and so a higher number of apodous segments than the females. Similarly, *Lepidurus bilobatus* has 33 segments, 60 pairs of appendages and 6 apodous segments (Linder, 1952), while *L. batesoni* with the same number of segments, but only 39–52 appendages, has 8–9 apodous segments.

The apodous segments were frequently counted in early descriptions of Notostracan species, and several specific distinctions have been based on small differences in this number. It is now known that there is so much variation in this character in *Triops* that it is useless as a systematic character ; the pure line *T. cancriformis* had a variation of three (5–7). It may be valid in some *Lepidurus*, and is of use in at least one specific distinction.

A few general rules can now be drawn from the data on segmentation and appendage number.

In both genera males often have a higher number of segments within a sample, while the reverse appears to be unknown. In 25 samples of *Triops* I found this to be the case, while in 21 the difference was insignificant.

Certainly in *Triops*, and probably in *Lepidurus*, the males tend to have fewer appendages and so a higher number of apodous segments than the females ; in 44 *Triops* samples the males had a higher number of apodous segments, in 7 there was no difference and in 1 the female had more.

Specimens with high numbers of segments tend to have a high apodous number in both genera.

Thus, it is obvious that these characters can be used in systematics only with a great deal of caution, and appear to be of more use in *Lepidurus* than in *Triops*.

(4) *Carapace*

The shape and size of the carapace in Notostraca varies considerably and the differences found have frequently been used in the past by systematists to distinguish species. Ghigi (1921) used the carapace shape as one of his arguments in separating *Triops* into two genera : *Thriops* and *Proterothriops* (*sic*) ; Barnard (1929) considered the shape to be a distinguishing feature between South African species of *Triops*, particularly between his *Apus numidicus* and *A. namaquensis*. On the other hand, Linder (1952) made no use of the carapace size and shape in his revision of the North American forms. The carapace is one of the structures which is usually described adequately in the earlier papers.

In each individual the growth of the carapace from the earliest larva is probably isometric; a number of individuals of *Triops cancriformis* and *T. granarius* were measured during the whole of their growth period and it was found that the ratio of carapace length to total length remained the same throughout growth. In the former species the growth coefficient (k) of the carapace was 1·02, while in the latter species $k = 1·01$; these results are shown graphically in Text-fig. 1.

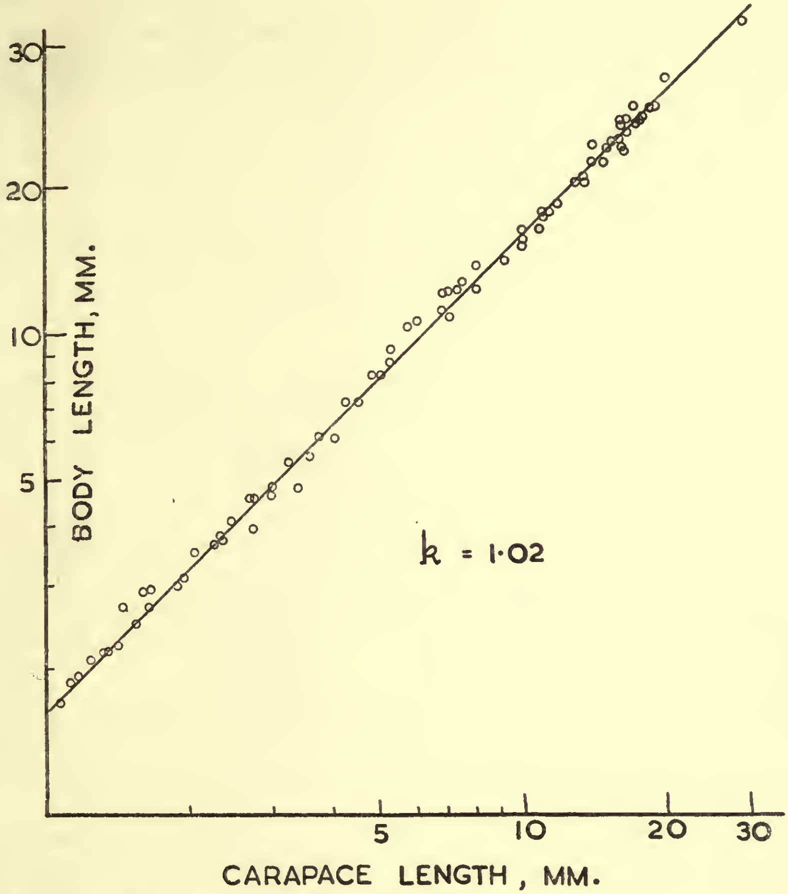

Fig. 1. Growth coefficient (k) of females of *Triops cancriformis* from Hampshire—five individuals.

The basic variation in the carapace is its size relative to the total length of the animal; in some forms it covers a much greater length of the body than in others; correlated with this relative size-difference are other differences in shape and strength of the carapace ; in those specimens in which it is relatively small it is always more rounded in outline, flatter, and less strong than in those in which it is large. These differences hold good for both genera.

The relationship between carapace length and total length depends both on changes in size of the carapace—the number of segments that it covers—and on changes in the number of abdominal segments. A comparison between two species of *Triops* made on the living animals illustrates this ; British female *T. cancriformis* have about 33 segments of which about 19 are exposed behind the carapace, which thus covers some 14 segments ; *T. granarius* from Johannesburg have, in the female, about 38 segments of which 27 are exposed, so that in this species the carapace covers about 11 segments. In the second species the increase in the number of exposed segments comes both from a shorter carapace and a larger number of abdominal segments. It is impossible to make such calculations on preserved specimens with any accuracy, because of contraction in the preservative.

The carapace appears to cover about 11–14 segments in most specimens, for on these segments are borne the most anterior of the spines which occur on the margins of the segments in the exposed portions of the abdomen ; in all the specimens examined, the first of these spines appear on segments 11–14, regardless of the total number of segments present.

Within a species, males have smaller carapaces than females, although this dimorphism is less marked in *Lepidurus* than *Triops*, and in shorter bodied than in longer bodied specimens of the latter genus. This sexual dimorphism in the carapace has been noted by many authors.

The dependence of the degree of this dimorphism on the number of segments means that while it is usually possible to distinguish males from females at a glance on this character within a population, males from short bodied populations may actually have longer carapaces than females from populations with high segment numbers. In the forms with the lowest numbers of segments the dimorphism may be so slight as to be virtually non-existent.

The carapace is smaller, more round, and flatter in populations of both genera which have relatively high segment numbers ; this is especially well marked in *Triops* where the specimens with the highest numbers of segments have remarkably small carapaces (Text-fig. 2).

Barnard (1929) maintained that the shape of the carapace was an absolute difference between his *Apus numidicus* and *A. namaquensis*, which he found in the former species to be oval in shape and in the latter almost round ; he also gave data on the number of apodous segments which show that *A. namaquensis* is longer in the body than the other species, although some overlap occurred between the two. He was concerned only with South African material, but on examining specimens of these species—and of synonymous ones—from the whole of their range in Africa and Asia I find that there is no discontinuity in the variation of carapace-shape. The round carapaces and the oval are connected by populations of intermediate form (Text-fig. 2A–E). The differences that Barnard found were differences between the long and the short bodied forms of the same species.

I can find no differences in the carapace shape or size which are not correlated

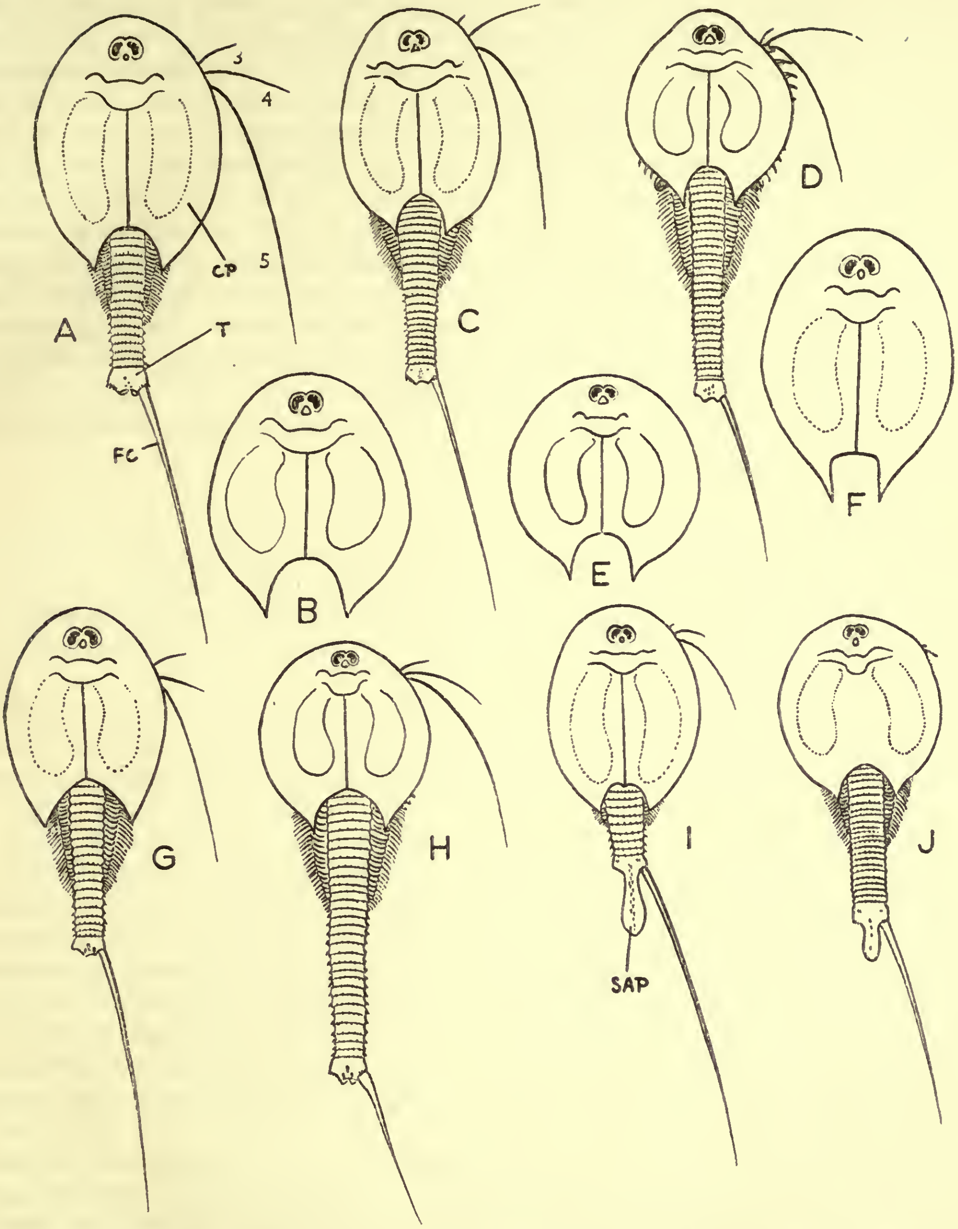

FIG. 2 Correlation of form with number of segments. A–E, *Triops granarius*, progressive increase of segments (32–42) ; F, squared sulcus on some specimens of *T. granarius* from South Africa ; G–H, *T. longicaudatus*, few and many segments respectively ; I, *Lepidurus apus* ; J, *L. batesoni*. (3, 4, 5, = endites of first thoracic appendage, *cp* = carapace, *t* = telson, *fc* = furca, *sap* = supra-anal plate).

with sex or the number of segments; *Triops cancriformis* tends to have a lower number of segments than *T. granarius* and so its carapace tends to be longer, less flat, than in the other species; and specimens of *T. granarius* with a low number of segments have carapaces similar in shape to those of *T. cancriformis*. *Lepidurus* spp. tend to have even shorter bodies and here the carapace may cover most of the abdomen, and may be so deep as to enclose the animal laterally.

The shape of the sulcus, or posterior emargination, of the carapace has frequently been described and importance attached to it; I find it to be very variable and can see no correlation with other characters; it may be shallow and wide in both long or short bodied forms, or small and round in similar animals. A peculiar squared sulcus has been seen in several short bodied populations of *Triops granarius* from Africa (Text-fig. 2F), but this grades into more rounded forms and is obviously of no significance. Wide, shallow sulcus shapes occur most frequently in *T. longicaudatus*, but this is of very doubtful value in the systematics.

The difficulty of an accurate classification of sulcus shapes makes it unlikely that this will ever be a useful character.

(5) *Carapace armature*

The carapace bears an armature of spines both scattered and localized. The whole outside surface may be smooth, or may bear scattered upright spines; the dorsal carina frequently ends in a spine and may bear smaller spines along its length; the sulcus generally bears a row of marginal spines, and the outside edge of the carapace may bear a similar row.

The carapace armature shows a great deal of variation, and has been referred to very frequently in past descriptions; some of this variation does seem to be of use systematically, but it must be used with caution and only as a confirmatory character in most cases.

The armature as a whole varies in its strength and development even within a population, and in some animals the whole armature is more strongly developed than in others—in the former not only are the spines larger and stronger, but they are also more numerous. In *Triops granarius*, when the scattered surface spines are well developed, the sulcus spines are particularly strong, the carina is denticulate and the whole carapace is more rigid than in other specimens. In a population of *T. cancriformis* from Tunisia (MNHNP) the armature of the exoskeleton is extraordinarily weakly developed, though typical of this species in arrangement, and extreme examples in this sample have no carinal or sulcal spines at all—a most singular condition.

The scattered spines on the surface of the carapace were features used by Sars in the description of two species of *Triops* (*Apus trachyaspis* and *A. sculleyi*, Sars, 1899), but Barnard found that specimens bearing such spines occurred sporadically among South African material. I have found such specimens in samples of *Triops granarius* and *T. longicaudatus*, both as isolated individuals and as complete samples. Specimens in which this character is well developed are so conspicuous—the carapace having a prickly feel—that I shall refer to them as the *trachyaspis*-form of whichever species is involved.

The terminal spine of the carina is most prominent in larval *Lepidurus*; I have seen specimens of *L. arcticus*, *L. apus apus* and *L. apus viridis* in which it is relatively enormous in the second and third instars (Text-fig. 13A). In larvae of *Triops* it develops later and is never as large as in young *Lepidurus*. The growth rate of this spine in *Lepidurus* must be strongly negatively allometric, for although it is present in most adults, it is relatively very much smaller in these than in the larvae ; in *Triops*, when it occurs, this spine has a positively allometric rate for it is quite small when it first appears, and becomes, in the adult, of a size relatively similar to that of adult *Lepidurus*.

This terminal spine occurs in almost all adult *Lepidurus* and is absent in only a few. There appears to be no correlation between its absence and other characters ; *L. batesoni* and some specimens of *L. apus apus* and of *L. apus lubbocki* are without it, but these specimens of *L. apus* are otherwise quite normal. There is probably a variation in the growth rate of this spine to account for its disappearance in adults of a few populations.

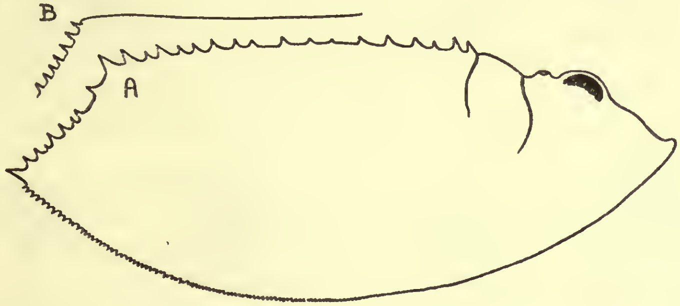

FIG. 3. Carapace of *Lepidurus lynchi*. A, typical form of carinal spines ; B, specimen with no carinal spines.

In *Triops* there is a loose correlation between the occurrence of the terminal spine and other characters ; within a species it is more commonly present in short than in long bodied forms. There is some difference between species, too, and as might be expected it is almost always present in the relatively short bodied species, *T. cancriformis*. It is present in the remaining species only in their short bodied forms.

The carina may bear a series of spines, most commonly at the posterior end just anterior to the terminal spine. These have frequently been used in the past for systematics (Ghigi, 1921 ; Linder, 1952) and they have proved to have value in certain cases. In *Triops* they may be present, or absent, in both long and short bodied forms, but there are some interesting differences within *T. cancriformis*. In this species a few small spines are generally present posteriorly, and these are more numerous and much stronger in specimens from Morocco and Southern Spain ; these are the populations referred to by Ghigi (1921) as *Thriops mauretanicus*, but they are now considered to comprise a sub-species (sens. Mayr, *et al*) of the more widespread *Triops cancriformis*. Another sub-species of this species is characterized by the complete absence of carinal spines.

In *Triops australiensis* and *T. longicaudatus* these spines are most frequently completely absent, but in a number of populations, that from the rice fields of Biggs County in California, for example, the whole carina bears an even row of very small denticles.

Most specimens of *Triops granarius* are without carinal spines, and only a few of the short bodied specimens have an arrangement like that of *T. cancriformis.* Very rarely this species has a long row of very small denticles like those of *T. longicaudatus.*

The majority of specimens of *Lepidurus* have perfectly smooth carinae but a remarkable series of large teeth along the carina occurs in *L. lynchi,* quite unlike anything else in the Notostraca (Text-fig. 3).

The sulcus normally bears a marginal row of spines, the only exceptions being some of the specimens of *Triops cancriformis* from Tunisia mentioned earlier. There is a fairly clear correlation of the form of these spines with the number of segments in *Triops*, but not in *Lepidurus* ; they are larger and fewer in number in short bodied forms of the former genus.

Their development in *Triops* is fairly clear ; the spines at the outside angles of the sulcus appear first, in the 4th or 5th instar, at which time the rest of the sulcus has a finely granulated margin. The first marginal spines appear in the 7th or 8th instar, and increase in number until about the 10th instar, after which time the number is fixed, though in a few specimens small subsequent additions may occur. There is little variation in this character in an individual after it is about 5·0 mm. in carapace length.

Barnard (1929) considered that there was so much variation between individuals in the sulcus spines that their use in systematics was not justified, although earlier writers had placed much emphasis on them. Linder admitted this variation, but thought that in some cases specific differences could be found.

I can discover no differences of the sulcal spines in *Triops* which can have any value in systematics, most of them are correlated merely with body length ; in *T. granarius,* short bodied forms have long, slightly curving spines and in longer bodied animals a larger number of small, blunt spines occurs. As in other characters *T. cancriformis* here resembles the shorter bodied *T. granarius* specimens.

In *Lepidurus,* a correlation with body length was not observed ; some specimens with 28 and some with 33 segments had small squat spines, but the vast majority of samples of all body lengths have long spines similar to those of *Triops cancriformis.* An unusual arrangement occurs in *Lepidurus apus packardi* in which the margin is closely set with many small squat spines like those of larval *Triops.*

The outer margin of the carapace in both genera normally bears a series of denticles which produce a finely serrated edge ; this is variable in development, and is normally stronger near the posterior angles of the carapace ; in only one case are these marginal denticles of any value systematically ; some specimens of *Lepidurus lynchi* bear a series of teeth along this edge which are very much larger than those of any other known form.

The amount of individual variation which may be expected in the carapace armature of a population was illustrated by the pure line of *Triops cancriformis* ; here the number of posterior teeth on the carina varied from 2–10, the number of sulcus spines from 24–32, and all the specimens had a large terminal carina spine.

(6) *Supra-antennal crest*

On either side of the ventral surface of the head there is a ridge, behind which is set the first antenna; this is the supra-antennal crest of Simon (1886), which Linder (1952) suggests may be worth study. I find it variable within a single species, in some specimens of *Triops c. cancriformis* it is denticulate and in others smooth and less prominent. It seems improbable that it is of importance systematically.

(7) *Eyes and dorsal organ*

In all adult Notostraca the dorsal surface of the head bears a pair of compound eyes, an ocellus, and the dorsal (or nuchal) organ.

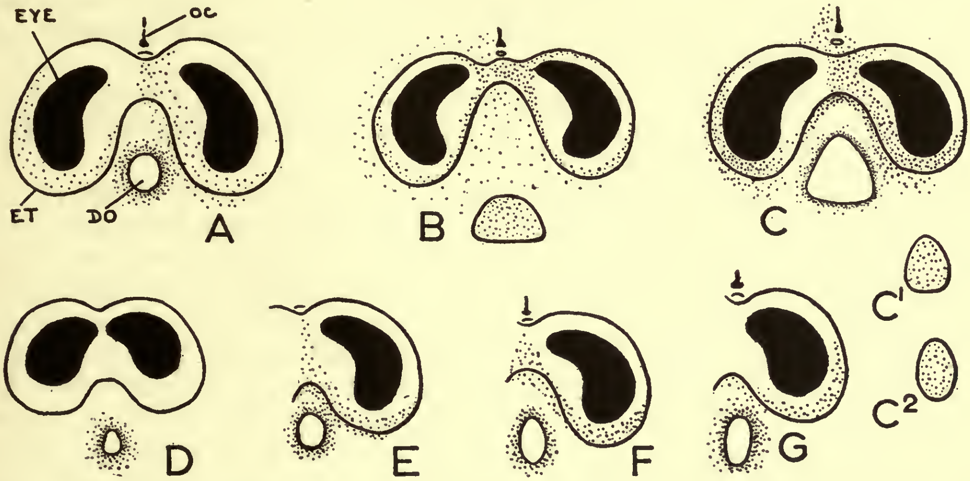

Fig. 4. Eyes and dorsal organs. A, *Triops cancriformis*; B, *T. australiensis*; C, C_1, C_2, *Triops granarius*; D, *Lepidurus batesoni*; E, F, *L. apus*; G, *L. arcticus*.

The size and arrangement of these structures are given in most specific descriptions and considerable importance has been ascribed to them, in particular to the dorsal organ; Barnard (1929) showed that the dorsal organ varied in South African material from a small round shape to a larger and triangular one. Further, he found that the small, round dorsal organs tended to be set on a tubercle in his animals, but that the triangular ones were less elevated and nearly flush with the surface of the head. These differences, to which he ascribed much importance in separating species, now appear to be another example of a character which is correlated with the number of segments, and which varies in a similar fashion in several species.

In all the species of *Triops* the specimens with a low number of segments tend to have small, round and elevated dorsal organs, and as the number of segments increases so the dorsal organ becomes larger, less elevated, and more triangular in shape (Text-fig. 4C–C_2).

This is well shown by *Triops granarius*; in specimens from South Africa with only 33 segments the dorsal organ is small and round, or slightly pear-shaped, as it is in specimens with 36–37 segments from Chufoo, China (both BMNH); in longer bodied specimens it is much larger and more triangular. In *T. cancriformis* the usual shape is round, but in some of the longer bodied individuals it approaches the triangular form of most specimens of *T. granarius*. *T. longicaudatus* is similar in this character to *T. granarius*, but in *T. australiensis* a peculiar wide shape, with a slight emargination of the posterior margin, occurs in a few specimens.

I have seen no specimens, and can find no records, of *Lepidurus* with triangular dorsal organs; here the round shape seems to be usual but in most species it varies from round to oval (Text-fig. 4). In *L. arcticus* a peculiarly long, narrow oval shape is common and this does not appear to occur in other species (Text-fig. 4G).

The growth rate of the dorsal organ is very strongly negatively allometric and this further complicates its use as a systematic character. In the larvae it is a relatively enormous structure so that in the first instar its median length is commonly about half that of the carapace rudiment (Text-fig. 13B).

During growth to adult size its linear increase is only × 2 or × 3 while the relative growth of the carapace is naturally very much greater. This negative allometry appears to continue throughout growth.

Linder made use of the relative arrangement of the eyes and the dorsal organ in his species of *Lepidurus*. He found that *L. lynchi* has the dorsal organ placed well behind the posterior boundary of the eyes and of the tubercles over the eyes, in contradistinction to the rest of the genus in which he found that the dorsal organ was placed in part between the eyes. *L. batesoni* sp. n. has the first arrangement (Text-fig 4D), but *L. bilobatus*—the other member of the long bodied group—has not.

In *Triops*, almost all the specimens examined had the anterior margin of the dorsal organ between the eyes, the only exceptions being 8 of the 12 samples of *T. australiensis* examined, in which the arrangement was precisely similar to that of *Lepidurus lynchi* and *L. batesoni* (Text-fig. 4B); in the other four samples it was normal. This may indicate that not too much reliance should be placed on this character in either genus as a primary distinction between species.

(8) *Telson*

The telson bears an armature of spines on both dorsal and ventral surfaces, and variation of these have commonly been used in the past for separating species (Packard, 1883; Ghigi, 1921; *et al.*).

The important spines on the dorsal surface of the telson fall naturally into four groups to which it is convenient to apply names (Text-fig. 5); around the bases of the furca are rings of *furcal* spines; on the posterior margin of the telson of the larvae the first spines to appear are large and are identifiable in the adult—the *posterior marginal* spines; the median area of the telson may bear a row of large spines or scattered smaller ones—the *median* spines; around the dorsal sensory setae are rings or arcs of *setal* spines.

The development, but not the origin, of these spines differs radically between the several species of *Triops* (Text-fig. 5), and the final arrangement is of the greatest importance in the systematics.

All the specimens of *Triops* which were available were examined on a geographical basis, and no account was taken of previous determinations of the specimens; it was found that there was a strong correlation between the spine pattern of the telson and the geographical distribution of the animals, but none with the sex or the number of segments.

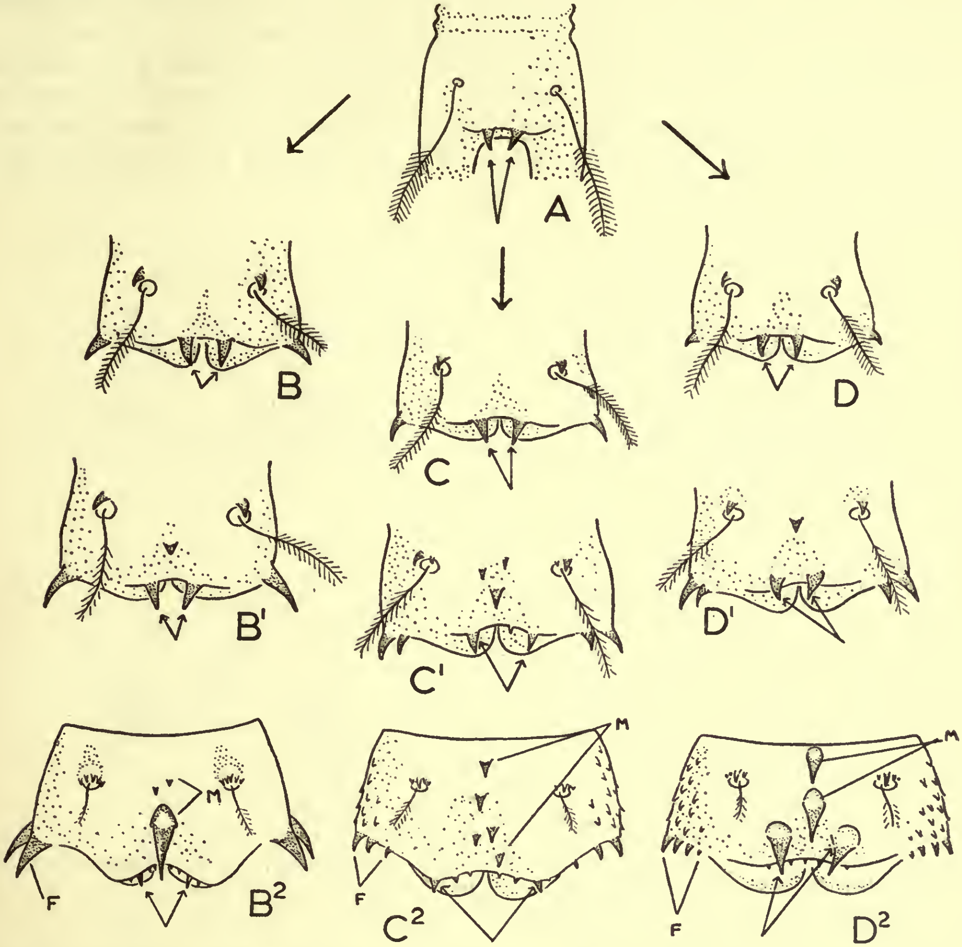

Fig. 5. Development of telson armature in *Triops*. A, larval stage (instar 2) common to all; B, C, D, instar 5–6; B_1, C_1, D_1, 3–4 mm. carapace length; B_2, C_2 D_2, adults. B_n, *T. cancriformis*; C_n, *T. granarius*; D_n, *T. longicaudatus* (the small arrows indicate the position of the posterior marginals in each case; *f* = furcal spines, *m* = median spines).

Without exception the specimens from Europe and western Russia have a small number of median spines arranged in an accurate row in the centre of the telson, the furcal spines are few and large, and the posterior marginals small, thin and remaining on the margin in the adult (Text-fig. 5A); this pattern occurs also in North Africa, the Middle East and northern India. In Africa south of the Palaearctic Region all the specimens have a larger number of small, relatively scattered medians in the mid-dorsal region, small, numerous furcal spines, and small posterior marginals (Text-figs. 5C, 6A). This pattern overlaps the European type in North Africa and the Middle East without forming intermediates, and then spreads across Central Asia to the Chinese coast. In North and South America the medians are similar to those of the European form, but there are two large spines, one on either side, at the posterior end of the median row, which represent the enormously enlarged and forwardly migrated posterior marginals, a fact which was confirmed by a study of the larval development (Text-fig. 5D). This form also occurs to the exclusion of others in the West Indies, the Galapagos, Oahu, and Japan ; a derivative occurs in New Caledonia (Text-fig. 16).

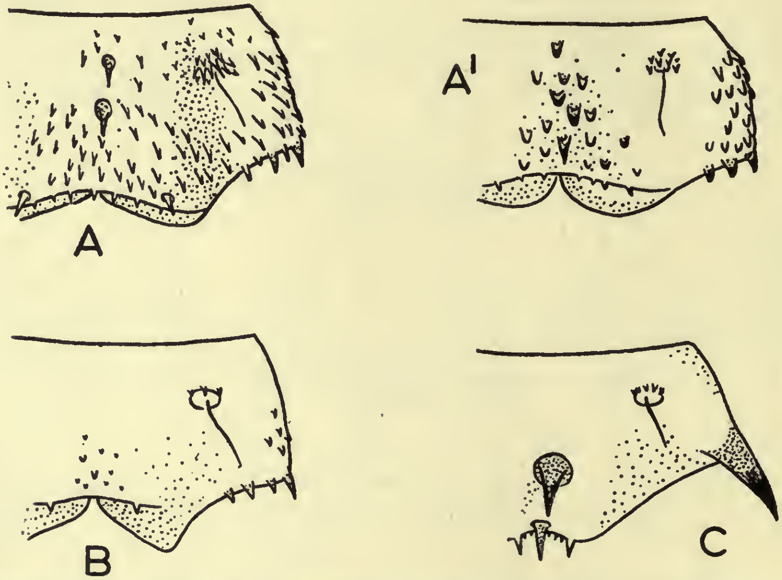

FIG. 6. Telsons of *Triops*. A, *T. granarius* (*trachyaspis*-form) ; A_1, *T. granarius* ; B, *T. australiensis* ; C, *T. cancriformis mauretanicus*.

The Australian forms have a very few small scattered medians, as in the African form, but they are so few in number as to be frequently absent (Text-fig. 6B) ; the rest of the armature is as in the African specimens.

This gives a picture of four large groups which are to a great extent allopatric, but forming where they overlap no intermediates. The descriptions in the literature completely confirm this grouping and are too numerous to list with profit.

As a systematic character this pattern appears to be perfect, there are no known intermediates, it is unlikely that it has any direct adaptive significance, and it is very easily seen in the specimens.

It must be remembered, however, that although the pattern is stable the numbers of spines which form it are very variable ; in the pure line *Triops cancriformis* there were 1–4 medians, 2–4 furcals, and, once, small additional posterior marginals barely distinguishable from the primary pair.

The number of these spines is fixed from a size of about 5 mm. carapace length, but as Text-fig. 5 shows, their relative sizes forming the true adult patterns are not stable until a little later, and allowance must be made for this (e.g. *Apus mavliensis*

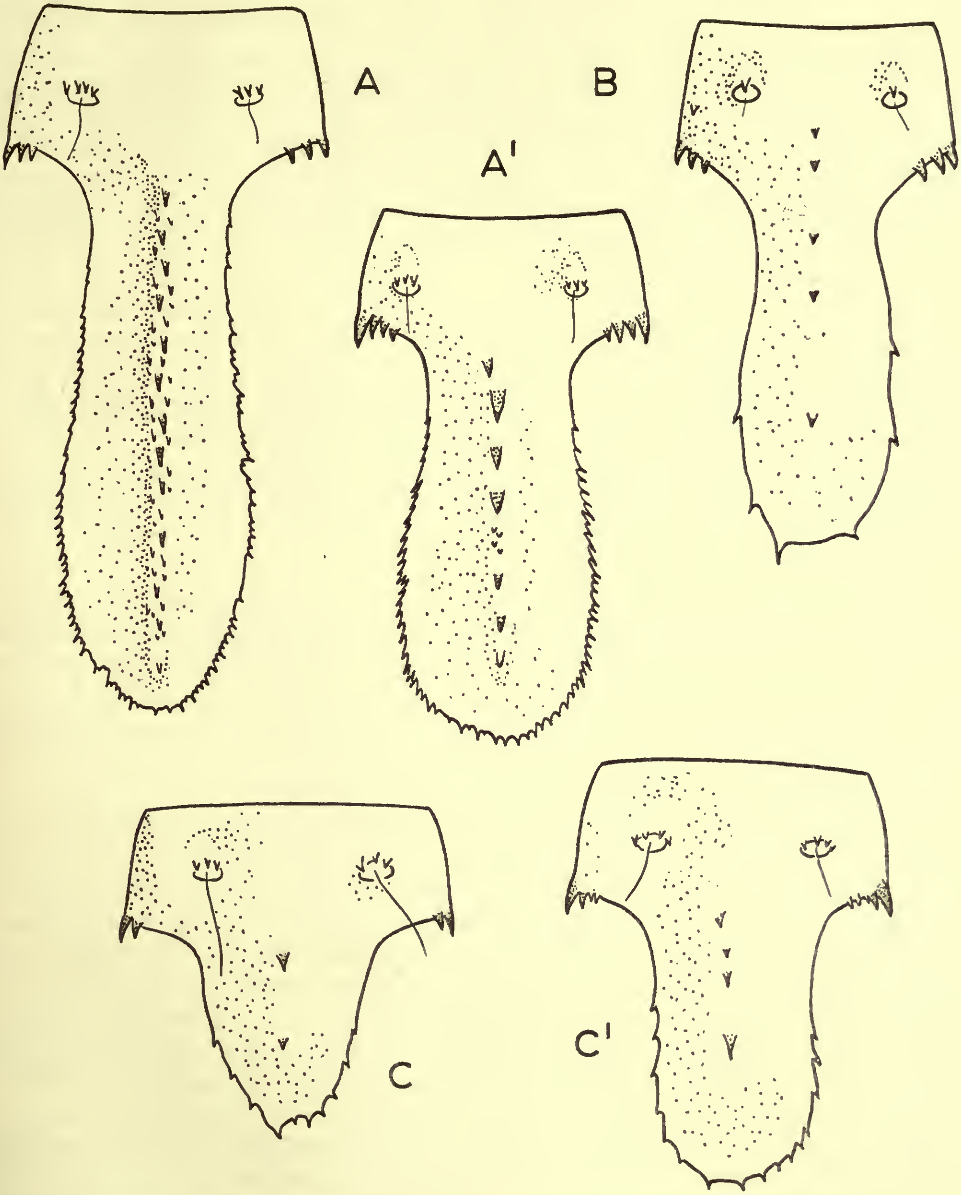

FIG. 7. Supra-anal plates of *Lepidurus*. A, *L. apus apus* ; A_1, *L. apus lubbocki* ; B, *L. batesoni* ; C, ♀, C_1, ♂, *Lepidurus arcticus*.

Tiwari appears to have a different telson pattern from the other Indian forms, but this species was described on immature individuals in which the posterior marginals were still relatively very large).

The spines encircling the dorsal setae are very similar in arrangement, though not in number, in all specimens of *Triops* examined, and no importance is attached to them.

In *Lepidurus*, the spines corresponding to these four groups can be recognized, but they are to some extent modified ; the posterior marginals are the first to appear in the larval telson (*L. apus*) and the posterior margin of the telson on which they are borne expands rapidly to form the supra-anal plate, carrying them with it, and they are soon indistinguishable from the other spines on the margin of the plate in most specimens. The furcal spines are similar to those of *Triops granarius* and do not differ much from species to species ; the setal spines are similar in form and lack of variation to those of *Triops* ; the medians form an elongate row along the mid-dorsal line of the plate.

This median series shows considerable variation and has frequently been used in the separation of species ; the number of spines increases to a certain extent as the animal grows (Linder, 1952) ; and this process probably continues until the animal is at least 15–20 mm. in carapace length, to judge from a sample from Berlin of *Lepidurus apus* (BMNH) consisting of large and small individuals.

The median spines may be borne on a slight keel, which is better marked in those specimens with a large number of spines in this series ; it is impossible to draw a line between presence and absence of a keel and contrary to Linder's opinion, I can make no use of it.

The number of spines in the median series is useful in the systematics of *Lepidurus* species, serving to distinguish the nominate race of *L. apus* from the other three sub-species. *L. arcticus* has a much lower number than the rest of the genus. These differences are not connected with the relative size in the adults of the supra-anal plate ; both *L. arcticus* and *L. lynchi* have relatively low numbers of medians, although the former has the smallest supra-anal plate in the genus and the latter one of the largest.

The marginal spines of the supra-anal plate vary in size and number and there is a connection between them and the median spines, when the latter are small and numerous, so are the former ; the marginals therefore are relatively large and sparse in *Lepidurus arcticus*, *L. lynchi*, and *L. batesoni* compared with the other species.

The size of the supra-anal plate itself varies between species—the most obvious difference being in *Lepidurus arcticus* where it is very small—but a great deal of the observed differences are due to age and sex ; males (Text-fig. 7C) have relatively longer and more spatulate supra-anal plates than females (*L. apus*, Braem 1893 ; *L. arcticus*, Sømme 1934) ; and the structure has a positively allometric growth rate throughout the period of growth (Braem, 1893 ; Campan, 1929).

The end of the plate is occasionally incised medianly, giving it a bilobed appearance ; this appears in several species and has no importance (Linder, 1952), and it is to be expected that this will occur in species other than those in which it has already been recorded.

The shape of the telson was used by Packard (1883), but Linder has shown that this is an unreliable character in *Triops*, though he records relative differences in length and breadth in some *Lepidurus* species. The variation is such that no reliance is placed on it here.

The dorsal sensory setae are present, and similar in form, in all species of Notostraca that I have examined, and are longer in small than in large specimens.

(9) *Segmental armature*

Each segment which is exposed behind the carapace bears a series of spines on its posterior border; this series is interrupted by the appendages and is continued ventrally only on the apodous segments.

The form of these spines on the ventral surface of the apodous segments has frequently been used in the systematics of both genera; Ghigi (1921) considered them to be important in *Triops*, as did Linder (1952) in *Lepidurus*.

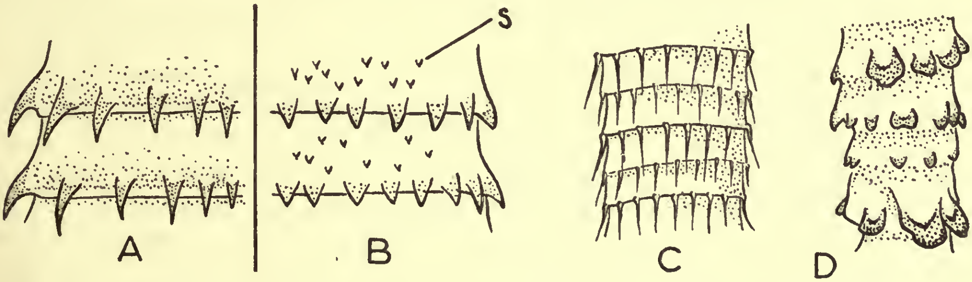

FIG. 8. Armature of apodous segments (A, B) and furca (C, D) of *Triops*. A, *T. cancriformis* without supernumeraries; B, *T. granarius* with supernumeraries (S); C, ♀ *T. cancriformis* or *granarius*; D, ♂, *T. granarius*.

On the ventral surface of these segments the spines near the midline are usually smaller and set more closely together than the lateral ones. Linder (1952) considers that the number and relative size of these centrals is diagnostic of certain species; he gives a variation of 13–28 teeth in *Lepidurus packardi*, *L. couessi*, and *L. bilobatus*, and only 8 in *L. lynchi*; I find the variation so great that this character is effectively useless even though the differences are at times striking.

In *Triops*, the shape of the marginal spines was used by Ghigi (1921), who found that they were squat in his *T. mauretanicus*, and finer in his other species; I find that the European and North African material—which Ghigi divided into species—shows continuous variation in this character although, as he described, there is a tendency for the Moroccan specimens to have squat spines.

These spines become rounded and heavy in males of *Triops granarius* in which the ventral armature of furca and telson are heavy; they are thus heavier in males than in females of the same species.

A more useful character on the apodous segments is the presence or absence of scattered supernumerary spines which occur between, and anterior to, the marginal spines and are much smaller than them (Text-fig. 8). In *Triops cancriformis* only one specimen has been seen which possesses any of these spines, a female from Palestine (coll. Goldschmidt) which had 3–4 small supernumeraries on one of the apodous segments. In the other species of *Triops* it is most unusual to find a specimen which does not possess at least a few supernumeraries on each apodous segment, and in the main there are 10–12 per segment.

I have not seen these spines in *Lepidurus*.

(10) *Appendages*

The appendages have been described in considerable detail for one species (*Triops cancriformis*, Lankester 1881), but with the exception of one character have been little used in systematics. The endites of the first thoracic appendage are drawn out into filaments of which the longest endite (the fifth) forms an antenna-like structure in most forms. The length of the endite 5 and the number of segments of which it consists have been described by too many past authors to list. Even recently small differences in endite length have been considered to have significance (Tiwari, 1952).

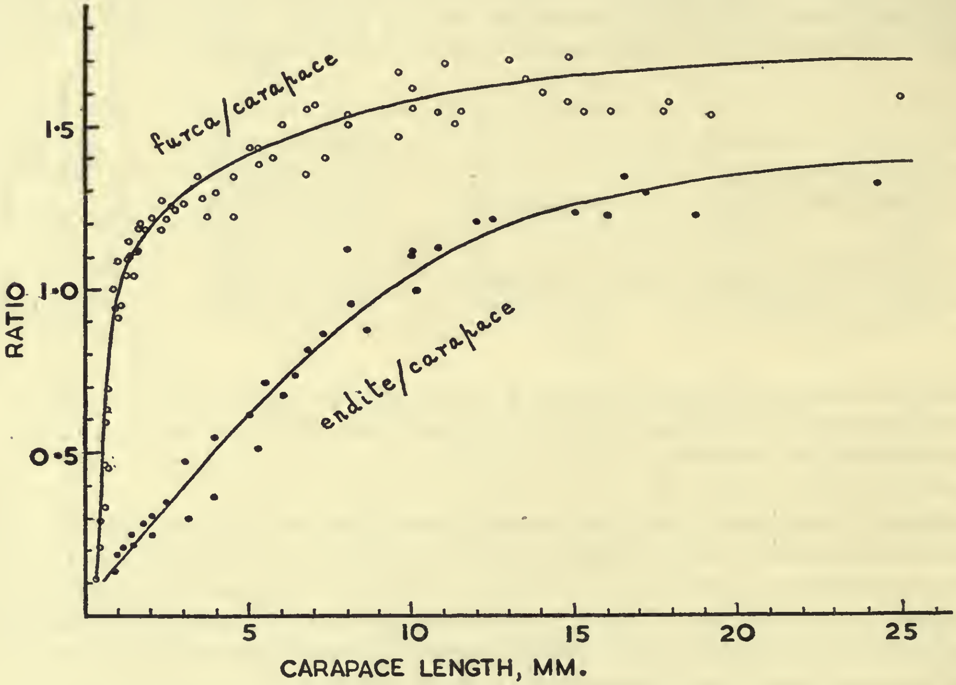

FIG. 9. Relative growth rates in *Triops cancriformis* from Hampshire. Furca and longest endite of first thoracic appendage expressed as ratios furca/carapace and endite/carapace for various carapace lengths. Any slope on the line thus indicates allometric growth, since the growth rate of the carapace is isometric.

A study of the developing endite of *Triops cancriformis* and *T. granarius* has shown that it grows positively allometrically and that this rate continues, to some extent, throughout life (Text-fig. 9). So small differences in relative length are of no use in systematics without much more investigation of the growth rates of this structure in many populations.

It is likely that the length of the endites is not related to the size of the animal *per se*, but to the instar that the animal has reached. Specimens which have grown rapidly, with a large increment at each instar would have a different endite length at a particular size from individuals with low instar increments due to poor conditions; this is borne out by the great size and relative proportional differences seen in laboratory cultures.

In museum samples, perhaps for this reason, the individual differences in this character appear to be greater than those to be expected between large and small specimens; if a sample is arranged in order of carapace-length the endite/carapace ratio does not increase evenly up the series, as would be expected from the results obtained from the growth of single specimens, and the inference to be drawn must be that the specimens have grown at different rates and are of different sizes at each instar.

This is further supported by the occurrence of two samples taken from the same locality in different seasons; two such samples from a locality in the Saône area of France (MNHNP) collected two years apart consisted one of large, the other of small adult individuals, but the endite/carapace ratio was very similar in each; in the first, individuals of 29–31 carapace length had a carapace/endite ratio of 0·80–0·84; in the second sample the same ratio occurred in specimens of 9·5–10·8 mm. in length.

The situation is further complicated by the fact that there is sexual dimorphism in the endite length; in 26 bisexual samples of *Triops*, 24 showed higher endite/carapace ratio in the males. This may be due to the relatively shorter carapaces of males than to any real difference in endite length relative to the total size of the animals. In living specimens this appeared to be the case.

It is very noticeable that the endites are shorter relative to the body length in both sexes of the longer bodied forms, but it is not possible to give reliable figures for this because of the parallel differences in the relative carapace length which renders inter-sample comparisons very difficult.

The range of the endite/carapace ratio is very great within a species determined as such on other characters; in *Triops cancriformis* this varies from 0·55–1·28, and in *T. granarius* from 0·47–1·52. No correlation with the geographical distribution could be found.

In *Lepidurus* the endites are not as long as in *Triops*. *Lepidurus arcticus* and *L. apus* form a series from animals with very short endites which scarcely project beyond the carapace, to those in which they are relatively long. In *L. batesoni* the arrangement is unique; the 5th endite of the first appendage is little longer than that of the second appendage, and the 6th endite forms a claw in both appendages although in all other Notostraca it is reduced to a small, soft lobe at the base of the 5th endite in the first thoracic appendage, undergoing negative allometry during growth (Text-fig. 10).

Linder (1952) remarks " . . . the legs of various species are known to be very similar to each other . . . " ; I can find no reference to a comparative study of the appendages of Notostraca, and so it seemed valuable to attempt at least a preliminary survey. Unfortunately, it is necessary to dissect the appendages from the specimen in order to examine them properly, and this has naturally been possible with only a few specimens. Appendages of representatives of both sexes of all four species of *Triops*, and of several of *Lepidurus* were examined after mounting in polyvinyl lactophenol.

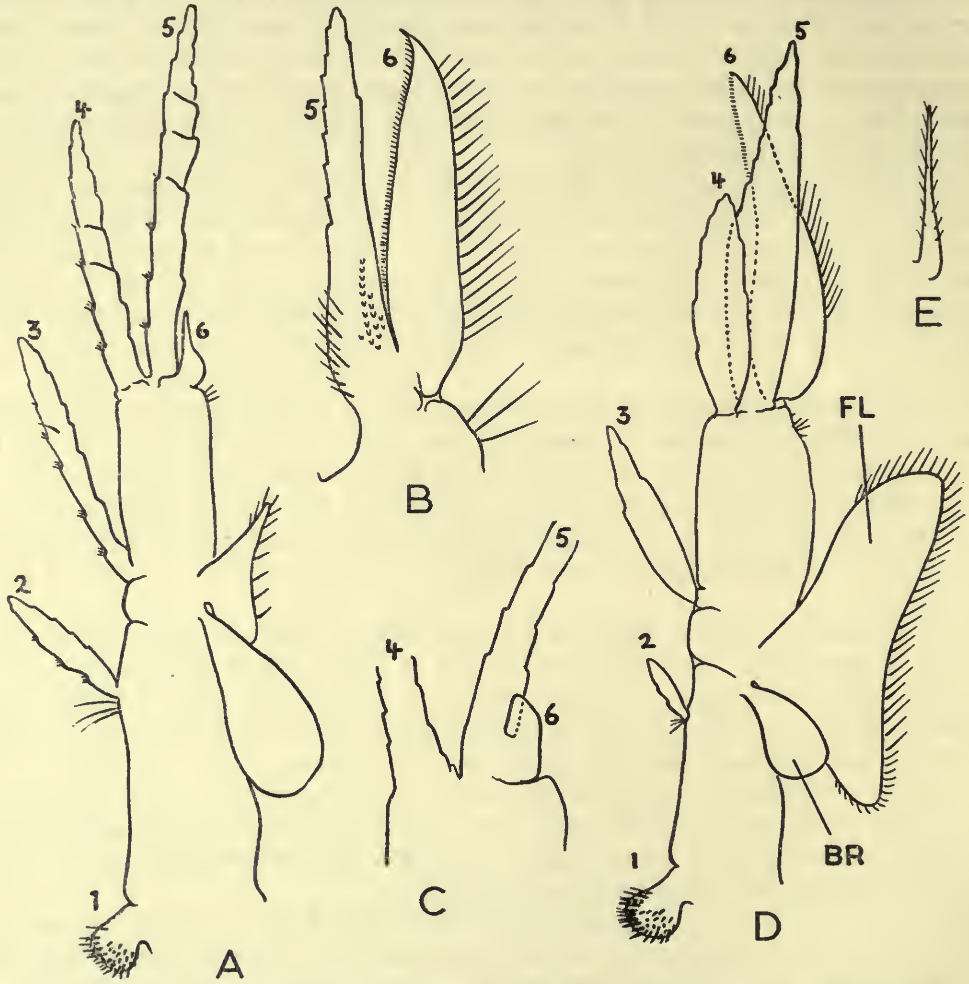

FIG. 10. Thoracic appendages : A, first thoracic appendage of *Lepidurus arcticus* ; B, tip of second thoracic appendage of *Triops cancriformis* ; C, tip of first thoracic appendage of *T. cancriformis* ; D, first thoracic appendage of *Lepidurus batesoni* ; E, endite 6 of first thoracic appendage of larval *Triops cancriformis*. (numbers = endites, *fl* = flabellum, *br* = bract.)

The first antenna is present in all larvae and adults and is remarkably uniform in structure; it bears at its tip three setae in all species that I have examined, although this number may be apparently altered by breakage. An aberration was seen in one specimen out of a sample of a *trachyaspis* form of *Triops granarius* from South Africa in which a pair of additional strong spines were present on one margin.

The second antenna must be present in all larvae, for in them it is the main locomotor organ; the form and numbers of setae are identical in the larvae of all four species of *Triops*, but I have been unable to make comparisons in *Lepidurus*; this appendage subsequently dwindles, due to negative allometry, and its locomotor functions are taken over by the thoracic appendages. It is often absent in large specimens, or it may be present (but very hard to detect) in the cleft in front of the mandible. I have found both conditions in large individuals of all species and can attach no importance to its presence or absence, contrary to the opinions of Linder (1952) and Spencer and Hall (1896).

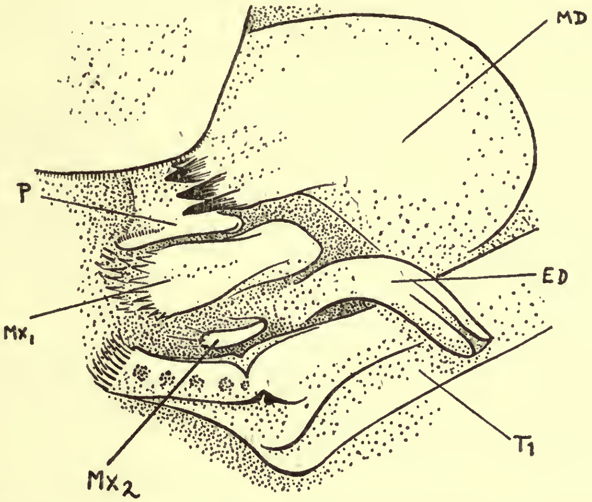

FIG. 11. Mouth parts of *Triops cancriformis* to show second maxilla. (*md* = mandible, *Mx1* = first maxilla, *Mx2* = second maxilla, *p* = paragnath, T_1 = first thoracic appendage, *ED* = efferent duct of shell-gland).

Ghigi (1921) used the arrangement and relative sizes of the teeth on the triturating surface of the mandible as a systematic character in his division of European and North African material; I have examined this character in many specimens conspecific with his material and there is so much variation that the invalidity of the character seems certain. Gauthier (1934) and Pérès (1939) found similar variation in their North African material.

The first maxilla has never been described comparatively; I find the main variation to be in the row of spines on the ventral edge of the appendage. These tend to be fewer in number and finer in *Triops cancriformis* than in the other species in the genus, but there is probably a complete gradation of intermediates, and I can make no use of the appendage in the systematics.

The second maxilla has received more attention than the previous appendage and seems to provide an important character (Text-fig. 11). Sars (1901) noted that the second maxilla was larger in *Lepidurus* than in *Triops*; this is so, and this appendage is also larger in *T. cancriformis* than in the other species of the genus, but even in this species is so small that it can scarcely be of importance in the feeding mechanism. Linder (1952) reported that it was absent in large individuals of most species of *Triops* (*australiensis*, *granarius*, *numidicus*, *longicaudatus*), but that no dwindling occurred during growth in *T. cancriformis*. I cannot agree with this. The second maxilla is present in all samples that I have seen of *T. cancriformis* and *T. granarius*, and absent in all those of *T. longicaudatus* and *T. australiensis*. Even in very small specimens of the latter two species it is absent; in a narcotized female from Morawa in Australia it was clearly missing, yet this specimen was only 7·5 mm. in total length.

In those species of *Triops* in which it is present it does not dwindle during growth; in a *T. cancriformis* of 8·0 mm. carapace length the second maxilla was 0·2 mm. long and in one of 18 mm. carapace length it was 0·4 mm. long; in a *T. granarius* of 7·5 mm. carapace length it was 0·13 mm. long, and in one of 13·8 mm. it was 0·33 mm.

Thus, the presence or absence of a second maxilla provides a clear character separating two species groups within *Triops*, but it is present and well developed in all species of *Lepidurus*.

The efferent duct of the maxillary gland arises at the base of this appendage, or from the position of the base if the appendage is absent; this duct is longer in *Triops* than in *Lepidurus* (Sars, 1901) and longer in male than in female *Triops*, in all the bisexual samples that I have examined.

The endites of the first thoracic appendage have already been dealt with, and I could find no significant variation in the other lobes of this appendage, except that the flabellum was relatively larger in *Lepidurus batesoni* than in other species—another character of the 2nd thoracic appendage appearing on the 1st in this species.

In the second thoracic appendage, the form of the terminal "claw" (= exopodite, Lankester 1881; apical lobe, Borradaile 1926; endopodite, Linder 1952; which I shall call endite 6 from the precisely similar ontogeny in the early stages of this and the other endites) was used by Ghigi (1921) to differentiate between species of *Triops*; I find great variety in the form of this lobe, but none that can be correlated with other characters. The relative lengths of endites 5 and 6 of this appendage show a sexual dimorphism; in males endite 5 is commonly longer than endite 6, while in the females they are more nearly equal. This is well known and I have been able to confirm it in all the bisexual samples that I have seen.

In the remainder of the thoracic series there is considerable variation in the shapes of the lobes of the appendages, but I can find none that are of importance between species; however, all the specimens that I have seen of *Triops granarius* from Central and Eastern Asia have endite 6 of the mid-thoracic appendages of a more rounded shape than is usual.

The armature of these appendages shows much variation in numbers of spines but not in their arrangement—a situation common in the armature on other structures in these animals. The numbers of spines in any group tend to increase during growth, but I have not been able to follow this closely.

The abdominal appendages showed no differences which might be of use systematically except to demonstrate once again a similarity between *Triops cancriformis* and the *Lepidurus* species; the flabellum of *Lepidurus* bears a number (20–30) of setae around its outer margin, and these are reduced in number in *Triops*. But *T. cancriformis* has a higher number (10–20) than the other species (e.g. *T. granarius*, 4–9).

Linder (1952) mentions an inflated condition of the flabella in some specimens; this I find to be due to post-mortem changes, especially in those animals which have died just after moulting, when the flabella are commonly so turgid with fluid after a few hours that they have the appearance of small red balloons.

(11) *Furca*

The length of the furca has been considered an important systematic character and was often included in even the early descriptions, but recent authors have thought it unreliable (Linder, 1952).

The furca grow very rapidly in the larval stages of *Triops* but their positive allometry soon becomes less marked, though some relative increase probably occurs throughout life (Text-fig. 9). The furca are generally relatively longer in those specimens in which the endites of the first thoracic appendage are long, and are probably correlated in their development with the number of segments in the same way as the endites. That there is no direct correlation with the endite length is shown by *Lepidurus arcticus* in which the endites are very short, but the furca are similar in length to those of the other species.

Gurney (1924) showed that sexual dimorphism in the armature of the furca occurred in *Triops*; the spines on the ventral surface of the proximal region of the furca tend to be broader in males than in females, in extreme cases forming protuberant scales (Text-fig. 8C, D). With few exceptions this dimorphism is more marked in long bodied forms, where the base of the furca tends to be relatively thick and rapidly tapering. In *Lepidurus* these spines are a little, but not much, thicker in males than in females.

PROTEIN SPECIFICITY

Oxyhaemoglobin has a characteristic absorption spectrum, and small differences in the wave-length at which the axes of the absorption bands occur have been demonstrated for several species of *Daphnia* by Fox (1945, 1946); similar differences in the position of the absorption band axes of the chlorocruorin of species and varieties of *Sabella* have been used systematically by the same author (1946).

The blood of Notostraca contains a considerable concentration of haemoglobin in solution and the size of the animals is such that a volume of blood sufficient for spectroscopic analysis can readily be withdrawn by a micro-pipette. It seemed profitable to determine the wave-lengths of the absorption bands of as many populations of Notostraca as were available, and to apply the results to the systematics.

A Hartridge reversion spectroscope was used to determine these wavelengths, in the manner described by Fox (1945), with a small refinement in technique to eliminate personal bias and errors due to parallax; the operator kept his eye to the instrument throughout a series of measurements and an assistant made the readings on the micrometer head and noted them down.

The wave-length of the axis of the oxyhaemoglobin-α band was determined by comparison with a sample of blood of similar optical density and of known wave-length (human blood, 5775Å). A number of readings were made on each sample of blood and the results were treated statistically.

Several cultures of *Triops cancriformis* from different European localities were compared, using several adults from each culture. The results (Table I) show that although there is little individual variation, the three populations are apparently different from each other; these differences gave a probability of significance of 0·02 when a *t* test was applied to them, and it may be taken that they are real and not referable to errors in the methods of measuring.

TABLE I.—*Wave-length of the axis of the oxyhaemoglobin-α band. Means of the readings taken on each animal, the averages of these means ($\overline{X}$), the number of readings per sample(N), and the standard errors of the means (S.E.). The figures in parentheses indicate the distribution of the readings within a sample.**

	Triops cancriformis			*T. granarius*		*T. longicaudatus*
	Sweden	England	Italy	Johannesburg	Grahamstown	California
Means per animal (Å)	5779·7 (30)	5778·3 (40)	5777·0 (20)	5776·7 (10)	5778·2 (30)	5777·3 (30)
	5778·9 (30)	5778·8 (30)	5778·2 (30)	5776·4 (30)	5775·5 (30)	5776·3 (30)
	5779·0 (30)	5778·6 (20)	5777·9 (30)	5776·8 (30)	5776·5 (30)	—
	5780·6 (30)	5778·8 (32)	5777·3 (30)	5777·3 (30)	5778·3 (30)	—
	5779·8 (28)	5778·9 (39)	—	5776·9 (30)	—	—
$\overline{X}$ (Å)	5779·6	5778·6	5777·6	5776·5	5777·1	5776·8
N	148	161	110	130	120	60
S.E.	0·356	0·305	0·281	0·340	0·370	0·255

This indicated that inter-specific differences must be considerably greater than these intra-specific ones to be of any value in systematics, and that many populations of a species must be tested before a value characteristic of that species could be determined.

In fact, subsequent inter-specific comparisons gave results (Table I) very little different from those obtained with *Triops cancriformis*.

The span between the axes of the oxyhaemoglobin and the carboxyhaemoglobin-α bands was also examined, for this is known to show differences between species in some cases (Fox, 1946). The results obtained with three species of *Triops* showed no differences which would justify further investigation. (span : *T. cancriformis* = 50·1 Å, *T. longicaudatus* = 48·2 Å, *T. granarius* = 47·5 Å).

The results of both these investigations are of no practical value in the systematics of these animals—the differences being much smaller than those found and used in *Sabella* by Fox—but do serve to demonstrate that in this character, as in others, the species of *Triops* form a remarkably closely related group.

* A single specimen of *T. australiensis* from Kalgoorlie was tested and gave a result of 5779·3 Å.

REPRODUCTION

It has long been known that some populations of Notostraca contain both males and females, and some only females. The occurrence of large populations in which no males could be found has generally been assumed to indicate parthenogenesis, especially since it was also known that isolated females from such populations could produce viable eggs.

Bernard (1889) found scattered testis lobes in the gonads of female *Triops cancriformis, Lepidurus apus* and *L. arcticus,* and reported these occurrences as cases of hermaphroditism. Zograf (1906) found ovarian tetrads developing in the testis walls of male *L. apus,* which must surely be an aberration of no use to the animal, for the oocytes subsequently degenerated. Spencer (1896) could find no testis lobes in the ovaries of *Triops australiensis.*

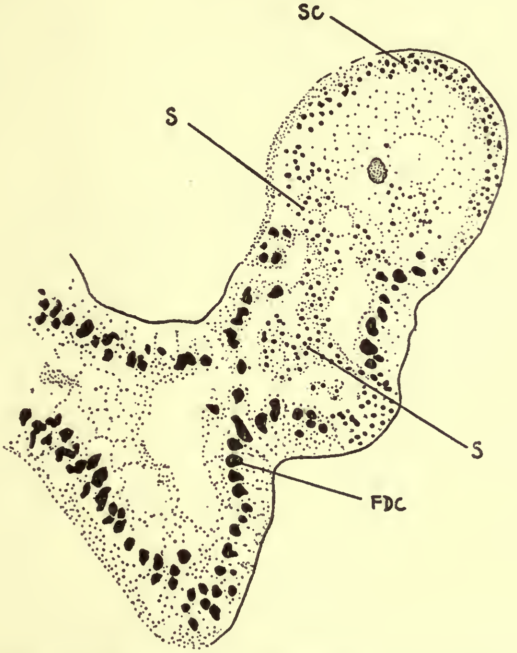

FIG. 12 Testis lobe in ovotestis of *Triops cancriformis.* 5µ section, Carnoy/Feulgen. (*S* = sperms ; *Sc* = spermatocytes ; *F.D.C.* = follicle duct cells).

Bernards' findings, largely ignored since his account, have been confirmed in the present work during investigation of the cytology of *Triops* and *Lepidurus,* and have been reported elsewhere (Longhurst, 1954). Hermaphroditism has been found in three species—*Triops cancriformis, T. longicaudatus* and *Lepidurus arcticus*—and it was found that females of the first two laid viable eggs in isolation and contained ovotestes (Text-fig. 12) ; no *L. arcticus* reached adult size. Females of *Triops granarius* and *T. australiensis* were unable to lay eggs in the absence of males, but did so readily as soon as males were put into the tanks with them and pairing had occurred; this was presumably correlated with the fact that no testis lobes were present in the ovaries of the females of these species.

There is no evidence to show that these latter two species of *Triops* are ever anything but bisexual; in all the material I have examined of these species the large samples invariably contained both sexes, and there are no records in the literature of females occurring in large numbers without males. In *T. cancriformis* there appears to be a complex situation: in the southern parts of its range bisexuality is normal, and a female from Algeria had no testis lobes; but in the more northerly regions males occur sporadically, often in very low proportions, so that some of the females probably reproduce without fertilization. In the extreme north of the range (Britain, Sweden) males are unknown and here females contain ovotestes. Unfortunately I have not been able to examine the gonads of females from a population with sporadic male occurrence. Mathias (1937) gives a review of the occurrences of males of this species.

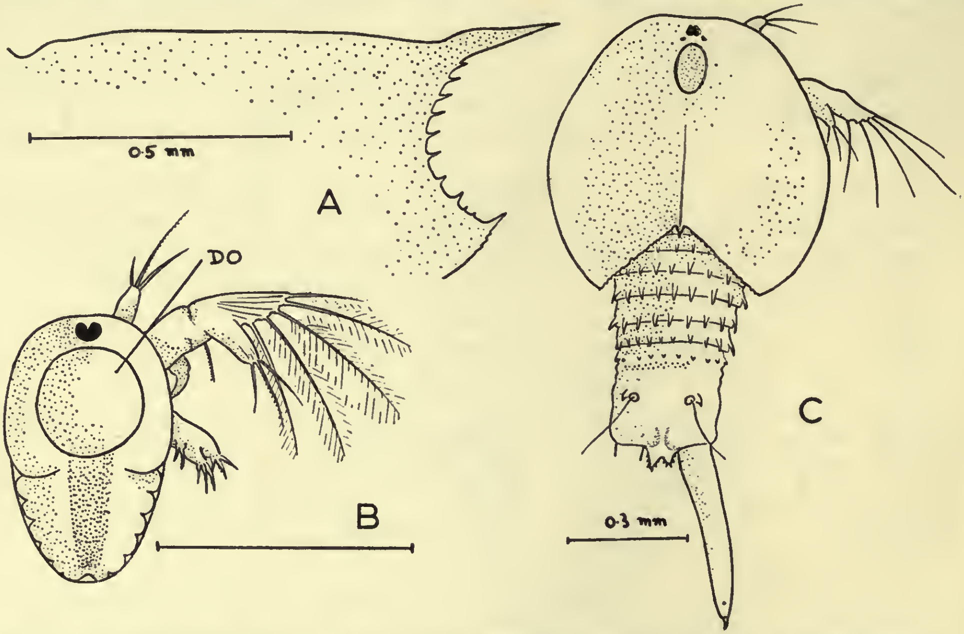

FIG. 13. Notostracan larvae. A = carina of instar 3 *Lepidurus apus*; B, metanauplius of *Triops cancriformis*; C, Neonatus of *Lepidurus arcticus*. (*do* = dorsal organ.)

In *Triops longicaudatus* the geographical distribution of males is not so clear; however, specimens from Californian rice fields where males are unknown contained ovotestes, and Linder (1952) reports examining many specimens from the Galapagos Islands without finding males. Uéno (1935) records this species in Japan and found no males in 78 specimens. It may be that all the populations of this species from the Pacific region are hermaphrodite, for the small samples that I have seen from Hawaii (Oahu) and from New Caledonia contained no males.

Reproduction in *Lepidurus* is less well explored ; it is known (above) that hermaphrodite individuals occur in some species, but males of these are also known in some populations although their geographical distribution is not clear. The three long bodied species all appear to be bisexual.

The size of the egg in *Triops* is variable, being larger in long bodied forms irrespective of species ; with this is correlated a size difference in the mature follicles in the ovary : *T. cancriformis* (33 segments), 0·28 mm. ; *T. granarius* (38 segments), 0·45–0·52 mm. This size difference is correlated with size differences in the resultant eggs and larvae, the long bodied forms having the largest larvae. In *Lepidurus* the differences may be even more marked and are diagnostic of species in at least one case ; the larvae of *L. arcticus* hatch at a later stage of development than those of the other species (Text-fig. 13), and the eggs are very much larger, the ovarian

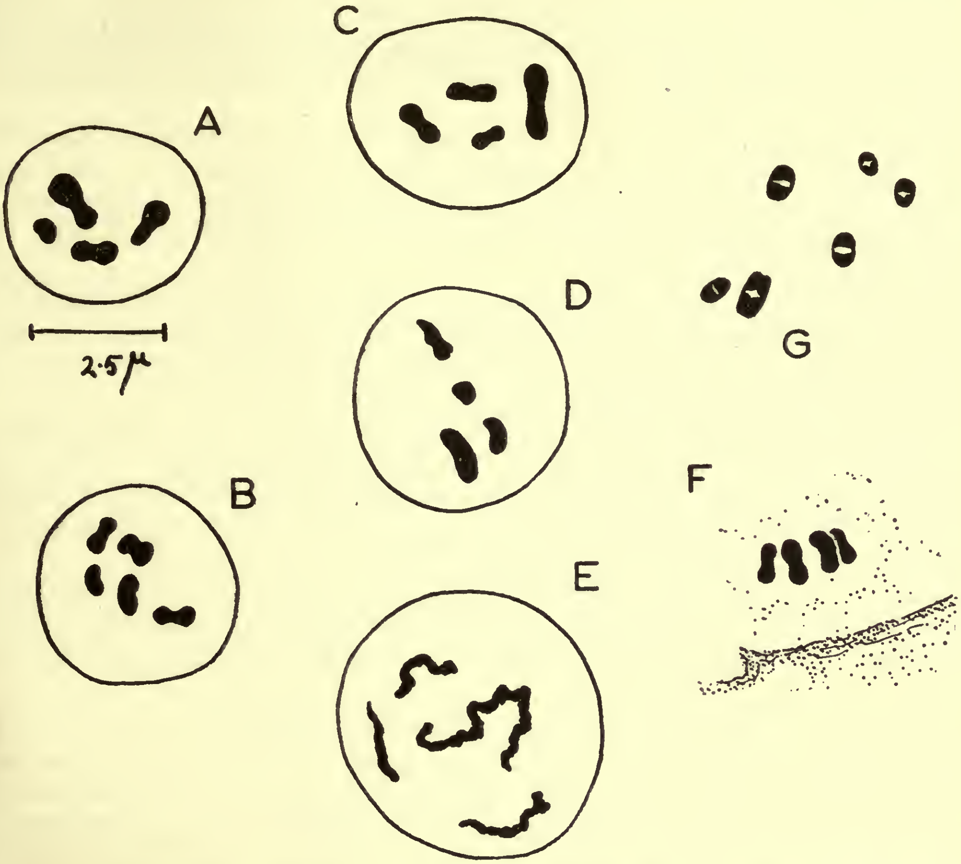

FIG. 14. Notostracan chromosomes. A–C, 2° spermatocyte telophase ; D–E, young oocyte ; F, resting unfertilized ovum ; G, spermatocyte diakinesis. A, *Triops longicaudatus* ; B, *T. australiensis* ; C, D, E, *T. granarius* ; F, *T. cancriformis* ; G, *Lepidurus apus*. (G is half the scale of the remainder and is redrawn from Goldschmidt, 1953.)

follicles are relatively few in number, large and elongated in form, and completely fill the space above the gut.

CYTOLOGY

Moore (1893) was the first to examine the Notostraca cytologically, and from observations on the divisions of somatic cells he concluded that *Triops cancriformis* was amitotic ($2n = 1$).

While the present work was in progress, Goldschmidt (1953) recorded chromosomes in the testes of *Lepidurus* sp. from Palestine, finding that aceto-orcein squashes gave diakinesis stages where $n = 6$ (Text-fig. 14G). I have since determined her material as *L. apus lubbocki*.

Using testis smears I found that two populations of *Triops granarius* from South Africa showed the number $n = 4$; this was most clearly seen in the telophase stages of the spermatocyte (Text-fig. 14C). This number was confirmed in females of the same populations in which a haploid set of chromosomes was readily seen in the very early oocytes (Text-fig. 14D, E).

Sections of the ovotestes of *Triops cancriformis* from the European cultures showed $n = 4$ in the oocytes, most clearly in the late oocytes or ova, resting in the longitudinal oviduct (Text-fig. 14E); squashes of the same gonads showed $n = 4$ in secondary spermatocyte telophases in the testis lobes.

In both of the above species of *Triops* the diploid number, $2n = 8$, was confirmed by finding mitoses in cells of the expanding follicle walls, at the stage of increase in size of the oocyte and nutritive cells. In *T. longicaudatus* from California the number $n = 4$ was seen in early oocytes (Text-fig. 14A) and in spermatocyte telophases, but it was not possible to confirm the diploid number.

A single male of *Triops australiensis* from Kalgoorlie was available and testis smears were made from it which showed, in the spermatocyte telophase, a complement of $n = 5$; this number was counted in at least 16 nuclei. The 5 chromosomes

TABLE II.—*Chromosome numbers of Notostraca*

	Haploid number		Diploid number
	Males	Females	Females
L. apus lubbocki	6 (diakinesis)	—	—
T. c. cancriformis	4 (2° spermatocyte telophase)	4 (resting oocyte)	8 (follicle duct epithelium)
T. granarius	4 (2° spermatocyte telophase)	4 (young oocyte)	8 (follicle duct epithelium)
T. l. longicaudatus	4 (2° spermatocyte telophase)	4 (young oocyte)	—
T. a. australiensis	5 (2° spermatocyte telophase)	—	—

in this haploid set are all sub-equal in length (Text-fig. 14B), and it seems probable that this situation could have arisen by the fragmentation of one chromosome in a set of four, such as the other species possess, in which one is nearly twice as long as the other three.

My findings and those of Goldschmidt are summarized in Table II, and both agree in ascribing a low number of chromosomes to the Notostraca so far examined. Moore's account of amitosis may be true of the cells that he studied, but even that is doubtful in view of my chromosome counts in epithelial cells ; his inference of a single chromosome was obviously incorrect.

All the *Triops* material was fixed in Carnoy's or Susa's fluids and was stained with the Feulgen reaction.

BIOLOGY

Very many accounts of the ecology of the Notostraca and of their appearance in temporary pools have been published, and a clear picture of their biology can be derived from the literature.

There appear to be almost no ecological differences between the species of *Triops*, a slight difference between *Triops* and most species of *Lepidurus*, and a marked divergence between *L. arcticus* and the rest of the Notostraca.

So far as is known, *Triops* occurs only in waters which dry out regularly, and the eggs normally hatch in the field only after a period of dessication. The habitat itself may vary a great deal in size from tiny rain pools and cart-ruts to large temporary lakes (Main, 1953) and the water may be fresh as in the Hampshire locality (Hobson and Omer-Cooper, 1935), brackish as in the Scottish pools (Balfour-Browne, 1909), or saline as in the lakes on the Tibetan plateau (Schlagintweit, 1872) and in Australia (Main, 1953).

The farming practice of rice fields makes these ideal situations for *Triops*, which are sometimes present in enormous numbers and have been recorded as a rice field pest from many parts of the world (they uproot the rice seedlings).

Lepidurus may occur in temporary pools, but there seems to be a tendency for most species to live in waters which dry out less regularly than the *Triops* pools. Lundblad (1920) records that *Lepidurus apus* is a spring form which appears when the temperature rises early in the year in ponds or ditches which have held water all the winter ; Linder (1952), on the other hand, says that he has seen the same species in Sweden in temporary pools. *L. apus viridis* occurs in a pool near Christchurch, New Zealand, which dries out in normal years, but is only very rarely found in neighbouring permanent ponds (G. Parry, personal communication). *Lepidurus* spp. regularly occur in temporary, often alkaline, pools in North America (J. Lynch, in litt.). L. Glauert has sent me a map showing all the records for *Triops* and *Lepidurus* in Western Australia and it is clear that *Lepidurus* is restricted to the south-western coastal belt where there is regular winter rain and *Triops* to the arid interior where rainfall is, at the most, sparse.

Lepidurus arcticus is confined to the boreal and alpine regions of the Holarctic, where it may occur in large lakes and form an important food of Salmonidae and where the eggs could never be dessicated (Sømme, 1934), it is also in pools which normally do dry out each year (J. Mohr, in litt.). The only other records of *Lepidurus* occuring in lakes refer to *L. lynchi* (Linder, 1952).

It has been thought that there is a difference between the two genera in the conditions necessary for the hatching of the eggs: Fritsch (1866) and Grasser (1933) thought that *Triops* eggs could hatch only after dessication, while Brauer (1877) believed that the eggs of *Lepidurus* were incapable of withstanding dessication. Schaeffer (1756) and Kozubowsky (1857) showed that the eggs of *Triops* were sometimes capable of hatching without drying out. This has been confirmed in the present work and it is now known that the eggs of at least three species of *Triops* can hatch out, after an interval for development, in the water in which they were laid, or will remain viable if dried out and will hatch when replaced in water. This accounts for the report by Mathias (1937) that *Triops* has two types of eggs: the one drought resistant and the other not.

Fox (1949) reported that the eggs of *Lepidurus apus viridis* were able to hatch after drying, and I have confirmed this with another mud sample from the same locality as his; *L. arcticus* from Iceland were also hatched from dried eggs. The ecology of *Lepidurus* outlined above indicates that the eggs of this genus must in many cases be drought resistant.

The eggs of *Triops* probably do not often hatch out without prior dessication, as the water must have a low osmotic pressure for this to occur, a condition unlikely to be found on the bottom of a pool where the eggs are laid, but most likely when the pool refills with water after rain and the eggs float to the surface.

SYSTEMATICS

From the analysis of the characters used in the systematics of the Notostraca it is evident that many of the obvious differences between individuals must be correlated with differences in the number of body segments (Text-fig. 2); in *Triops* there is no discontinuity in the variation of this number, so that neither the number itself nor characters correlated with it can validly be used in the separation of species.

In this genus, as the number of segments increases to give a long bodied form so the carapace becomes smaller, rounder and flatter; the number of legs remains about the same and consequently the apodous number becomes higher; the furca, and the endites of the first thoracic appendage become relatively shorter; the dorsal organ becomes larger, less elevated, and more often triangular in outline; the sulcus spines become smaller and more numerous, and the terminal spine of the carina is more frequently absent; sexual dimorphism becomes more marked.

Similarly, certain characters are correlated with the sex of the specimen; males tend to have more segments than females and so the characters outlined in the previous paragraph vary from male to female within a population; characters other than these also show sexual dimorphism: the efferent duct of the shell gland is longer in males than in females; endites 5 and 6 of the second thoracic appendage are more nearly equal in length in females; the 11th thoracic appendage bears a brood pouch in females; the ventral armature of the furca of males is coarse, often forming scales rather than spines, and with this is correlated the ventral armature of the telson and apodous segments, which vary in the same way between males and females.

These two considerations then—segment number and sex—invalidate a number of characters in the systematics of *Triops*. With those that remain there appear to be good grounds for dividing the genus into four groups, each with a geographical basis. The valid characters appear to be : the armature of the telson, the presence or absence of the second maxilla, and the arrangement of the eyes and dorsal organ. Of these the most important is the armature of the telson, which is diagnostic for each group ; the other characters, together with a few less well-marked ones, confirm this primary grouping.

Two groups are partially sympatric, and here there is no tendency to hybridize and no intermediates have been found in the areas of overlap ; there is a record, moreover, of two species—which correspond to two of these groups—living in the same pools in several localities in Morocco (Pérès, 1939). These two forms, therefore, behave precisely as biological species (*sensu* Mayr, 1942) would be expected to do when they become sympatric ; it seems justifiable to consider them, therefore, as species and since the degree of morphological difference between all four groups is similar to that found between these two, then all four may equally well be regarded as species.

Each species, then, has a geographical basis and a clear cut character in the telson armature, but contains populations which are remarkably different in general appearance depending on the number of body segments in the specimens. What determines the body length is completely obscure, for there appears to be a general tendency for the longer bodied animals to occur in the warmer regions of a species range, but there are many blatant exceptions to this generality ; Barnard's *Apus ovamboensis* is a population of exceptionally short bodied *Triops granarius* from a very hot and dry part of Africa.

It is likely that an experimental study of the effect of environmental factors on morphology would throw some light on this problem, for perhaps the effects are seen only after a considerable number of generations.

Several species show some indications of the presence of geographical races ; the differences between these are much slighter than the specific differences, and their distribution indicates that the geographical barriers between them are very slight. *Triops cancriformis* will serve as an example ; the populations in Morocco and southern Spain differ in several respects from the rest of the species, even though in Spain there is no geographical barrier where the change occurs, and there is some evidence that intermediates occur where the races meet, for in Seville and near Gibralter the specimens are identical with the Moroccan ones and from Valencia they are similar to the specimens from the rest of Europe, but in Ciudad Real—midway between the two areas—the specimens are intermediate. A similar zone of intermediates seems to occur in Spanish Morocco east of Ceuta.

Ghigi (1921) considered these races of *Triops cancriformis* to be species and described them as such ; Colosi (1922) and Pérès (1939) referred to Ghigi's species as varieties of the single species *T. cancriformis* but Gauthier (1934) used a true trinomial nomenclature and considered them to be sub-species or geographical races ; I follow this nomenclature and believe them to be sub-species in the sense that Huxley (1942) and Mayr (1942) used the term.

The arrangement of the species seems to follow different principles in *Lepidurus* from that in *Triops*, and the following account owes very much to the work of Linder (1952) who demonstrated the existence of two species-groups within the genus, each group characterized by its segment numbers.

The variation in segment number in *Lepidurus* is not so great as in *Triops*, and many characters show no correlation with this number in *Lepidurus* though the correlation is obvious in *Triops* : the armature of carina and sulcus ; the endites of the first thoracic appendage ; the number of apodous segments and the size and shape of the dorsal organ. The segment number shows a marked discontinuity at about 30 ; the vast majority of specimens have less than this number, and those which have more are aberrant in other respects.

Within the short bodied group there is relatively little differentiation, but *Lepidurus arcticus* can be separated at once, and is distinguished by its range, its habitat, its relatively short supra-anal plate and endites. The remainder of the group appears to comprise a single species, with a few rather ill-marked, but very widespread, sub-species.

Linder (1952) showed that *Lepidurus couesii* was conspecific with specimens determined as *L. macrourus* Lilljeborg. I can find no differences between the specimens that I have seen of either of these species and those of the European *L. apus*. The ranges of variation in the segment number are similar, the size and armature of the supra-anal plate is the same, and so is the armature of the carapace.

In California a form occurs which is admitted as a species by Linder, *Lepidurus packardi* ; in these specimens there is usually a slightly higher number of segments than in the normal *L. couesii* (= *L. apus*), the apodous number tends to be higher, and the sulcus spines are very small, numerous and closely packed. In the Mediterranean region there occurs a form which diverges from typical *L. apus* in a similar way except that the sulcus spines are normal. Both of these forms replace the typical race over very restricted areas, but there appear to be no effective geographical barriers separating the several ranges from one another, and for these considerations I propose to consider these forms to be sub-species of the typical and widespread *L. apus*.

The Australasian forms do not differ from typical *Lepidurus apus* as much as do the above two sub-species, and many specimens would be indistinguishable if placed in a sample from Europe. However, I have seen no specimens which have the high number of central spines on the supra-anal plate which are very common in the typical *L. apus*, so that there is a slight degree of morphological differentiation and I propose to consider the Australasian form as another sub-species, *L. apus viridis*. The South American forms which I know only from descriptions must be considered as another sub-species of *L. apus*.

The rest of the genus comprises the few longer bodied specimens which are known. All have coarse and sparse marginal spines on the supra-anal plate—a character which they share with *Lepidurus arcticus*—and a low number of central spines on the same structure ; specimens from three localities bear uniquely large spines on the carina and the carapace margin and these are Linder's *L. lynchi*, typical form and var. *echinatus*. A small sample from Russia has a considerably higher apodous number than the rest of this group and shares with *L. lynchi* a peculiar arrangement of the eyes and the dorsal organ, which resembles the arrangement in *Triops australiensis* where the anterior margin of the dorsal organ may be placed well behind the posterior margin of the eyes. A single specimen from Utah was placed in this species-group by Linder on account of its segment number and seems to agree with the description of *Lepidurus bilobatus* Packard, having a normal carapace armature and normal arrangement of the eyes and dorsal organ. The only possible arrangement at the moment is to consider all these three forms as three separate species, but it seems very probable that future work will be able to find a connection at least between *L. bilobatus* and the Russian sample (*L. batesoni* sp. n.) and perhaps between these and *L. apus*.

It will be noted from the foregoing account how widespread are the species of the Notostraca and this is probably accounted for, as it is in some other invertebrates, by their passive distribution ; the dried viable eggs must be blown around by wind, and transport by birds is not unthinkable, for the eggs when laid are extremely sticky and remain so for some days while the shell hardens, and so could presumably adhere to larger animals, The eggs of other phyllopods are known to be capable of passing unharmed through the guts of amphibia (Mathias, 1937), and birds are known to eat Notostraca ; starlings (Decksbach, 1924) and gulls (Balfour-Browne, 1909) are recorded as feeding on *Triops cancriformis*, and Summerhayes and Elton (1923) watched Arctic terns feeding *Lepidurus arcticus* to their young, and thought that they might drop them accidentally into fresh pools on their way to the nest.

A passive distribution such as this must mean that geographical barriers are not nearly so effective as they are for sedentary, or non-passively distributed animals, and has produced species with world-wide distribution in other animals, such as Tardigrades and Rotifers.

In addition, the group has a very long geological record and has had ample time to occupy all suitable areas ; fossils from the Permian (Guthorl, 1934) are clearly Notostracan carapaces, and forms from the Triassic of Europe (Trusheim, 1938) are certainly *Triops* and differ from extant *T. cancriformis* only in the small size of the terminal carinal spine. The upper Triassic *L. stormbergensis* (Barnard, 1929) from South Africa is very similar to recent species except that the supra-anal plate has, apparently, no central spines as in some extant *L. arcticus*.

It is impossible from these few fossils to give any account of the history of the group, except to point out how little evolution has occurred in the space of 170 million years since the Triassic forms were alive.

However, something can be deduced about more recent changes in distribution. During the Pleistocene glaciations *Lepidurus arcticus* was much more widespread in western Europe than it is now ; this species is known from lacustrine beds of that time from Scotland (Bennie, 1894) and from the Isle of Man (Geikie, 1894), and now shows in Scandinavia the typical distribution of a boreo-alpine relict occurring at sea level in the North and at progressively greater altitudes towards the South (Sømme, 1934).

Triops cancriformis must have been absent from much of its present range at the same period, and the post-glacial extension may have been performed largely by hermaphrodites, which predominate in the northern parts of its range; for these would be more efficient in dispersal as only a single egg would be required to effect a colonization. Perhaps the increasingly sporadic occurrence of males towards the north indicates a spread northwards of bisexuality.

All the known rice field populations consist entirely of females (or hermaphrodites if parthenogenesis is assumed not to exist in these animals) and this strengthens the above argument, for these are relatively new habitats for Notostraca, and a colonization by hermaphrodites ahead of the bisexuals seems to have occurred.

The westward extension of *Triops longicaudatus* across the Pacific from the largest area of distribution in North America, may also be of relatively recent origin and has apparently been performed again by hermaphrodites, for no males are known from the Pacific populations (p. 47).

Nomenclature

Keilhack (1909) and Fox (1949) have shown that the generic name *Apus* Schaeffer, 1756 should be rejected in favour of *Triops* Schrank, 1803; this practice will both accord strictly with the Rules of Nomenclature and will avoid further confusion in this genus, and in the avian genus *Apus* Scopoli, 1777. I therefore propose to follow Keilhack in the use of *Triops*.

The use of trinomials is necessary to describe formally the geographical sub-species recognized.

The lists of synonymies before each species are not complete lists of references to that species, for these would be too long and not very useful—but include (*a*) the names, and the various spellings of each name, that have been applied to that species, and (*b*) important descriptive works.

Apus has been applied to Crustacea other than Notostraca; *Apus pisciformis* Schaeffer is an Anostracan and *Apus caudatus* De Kay, was a crustacean parasitic on a crab.

Identification

The following key should serve to identify specimens down to species, but the user must bear in mind the extent of variation in any character and not expect the figures to match the specimen in details of armature. It would be very valuable if the segment number, the apodous number, and the number of appendages were given in any future records.

It must also be remembered that every individual in a sub-species may not be typical of it; many ornithologists consider a sub-species to be valid if 75% of its specimens can be placed in it without question. In *Triops cancriformis*, for example, it may be difficult to ascribe single specimens to the nominate race or to *T. cancriformis simplex*, for the smooth carina which is typical of the latter occurs in some individuals of the former, but I have no knowledge of whole samples of the nominate race with smooth carinas.

Key to species of Notostraca

1. Supra-anal plate present (Text-fig. 7) . . . . (*Lepidurus*) 2.
   Supra-anal plate absent . . . . (*Triops*) 6.

2. Segments more than 30 . . . . 3.
   Segments less than 30 . . . . 5.
3. Anterior margin of dorsal organ between eye tubercles (Text-fig. 4E) *L. bilobatus* (p. 53).
   Anterior margin of dorsal organ well posterior to eye tubercles (Text-fig. 4D) . . 4.
4. Carina and/or lateral margins of carapace with large spines. (Text-fig. 3) Apodous segments 3–5 . . . . *L. lynchi* (p. 53).
   Without large spines on carina or lateral margin. Endite 6 of first thoracic appendage as in Text-fig. 10D. Apodous segments 8–9 . . . . . *L. batesoni* (p. 54).
5. Supra-anal plate short, 0–5 spines centrally, marginals few (Text-fig. 7C). Endites scarcely project beyond edge of the carapace . . . . . *L. arcticus* p. 52).
   Supra-anal plate long (Text-fig. 7A, B), 4–100 central spines, marginals numerous. Longest endites with 3/4 of their length projecting beyond edge of carapace (Text-fig. 2*i*) . . . . *L. apus* (p. 50).
6. Second maxilla absent . . . . 7.
   Second maxilla present (Text-fig. 11) . . . . 8.
7. Posterior marginals sub-equal to medians and well forward of the margin (Text-fig. $5D_2$). Medians large, 1–4 in number, in a row . . . *T. longicaudatus* (p. 46).
   Posterior marginals reduced and marginal. Medians small, scattered when more than 3–4, often absent. (Text-fig. 6B) . . . . . *T. australiensis* (p. 48).
8. No supernumerary spines on the apodous segments (Text-fig. 8A). Medians large, 1–4, in a row (Text-fig. $5B_2$) . . . . *T. cancriformis* (p. 41.)
   Supernumerary spines present on apodous segments (Text-fig. 8B). Medians of various sizes, scattered except when less than about 5 are present, when they form an irregular row (Text-figs. $5C_2$, 6A, A_1) . . . . . . *T. granarius* (p. 44.)

Genus ***TRIOPS*** Schrank, 1803

1756. *Apus* Schaeffer (in part).
1758. *Monoculus* Linn. (in part).
1803. *Triops* Schrank.
1921. *Thriops* (sic.) Ghigi.
1921. *Proterothriops* Ghigi.

Triops is at once separable from *Lepidurus* by its lack of a supra-anal plate; even if a structure resembling a rudimentary plate (Text-fig. 7C) is found in some specimens of *Triops cancriformis* (Linder, 1952) there is never any doubt as to which genus a specimen belongs.

Proterothriops was erected by Ghigi for the reception of the long bodied forms of the genus; he was struck by the great difference in general appearance between long and short bodied forms which I have now been able to show to be conspecific in a number of cases.

Binoculus Geoffroy, 1762 and *Apodis* Zaddach, 1841, are not in a strict binomial system and are ignored on this account.

Triopes Schrank, 1803, appears later in the publication than *Triops* and must be regarded as a spelling lapse.

TRIOPS CANCRIFORMIS (Bosc)

1756. *Apus cancriformis* Schaeffer (in part).
1758. *Monoculus apus* Linn. (in part).
1801. *Apus cancriformis* Bosc.

1801. *Apus viridis* Bosc.
1803. *Triops palustris* Schrank.
1816. *Apus montagui* Leach.
1871. *Apus himalayensis* Packard.
1885. *Apus halicienis* Fiszera.
1885. *Apus lublinensis* Fiszera.
1885. *Apus varsovianus* Fiszera.
1909. *Triops cancriformis* (Bosc) Keilhack.
1909. *Apus cancriformis bidens* Sidorov.
1909. *Apus cancriformis transcaucasicus* Sidorov.
1921. *Thriops simplex* Ghigi.
1921. *Thriops mauretanicus* Ghigi.
1921. *Thriops apulius* Ghigi.
1922. *Thriops cancriformis* var *simplex*, Colosi.
1953. *Triops cancriformis simplex* (Ghigi, 1921) Margalef.
1953. *Triops cancriformis mauretanicus* (Ghigi, 1921) Margalef.

TYPE. Original is unknown, and designation of neotypes desirable. A sample from Kirkudbrightshire is selected (BMNH, 1907.10.17.1–4) and consists of a number of neoparatypes.

RANGE. Western Europe (Spain to Sweden) east to Russia; North Africa, Balkans, Asia Minor, Middle East to India. Individual records too numerous to list; Lundblad (1920) gives many for Europe, Decksbach (1924) many for Asia. Does not extend beyond 60° N and range in Russia obscure, but no records authenticated for Eastern Asia.

HABITAT. Temporary fresh or brackish waters; occurrence depends on the pools filling when the temperature is high enough for development, so usually summer form in Europe, spring form in N. Africa.

Rice field pest in N. Italy, Spain and La Carmargue.

DESCRIPTION. *Head.*—Dorsal organ round, oval or rarely triangular, small and with its anterior margin between the eyes. Second maxilla present in all specimens examined and relatively larger than in the rest of the genus.

Carapace.—Shape generally oval, more round in males. Carina with terminal equal to, or longer than, sulcus spines (Text-fig. 15); sometimes number of smaller spines on posterior carina. Sulcus spines long, 24–44, usually about 30.

Body.—Segments 32–35 in both sexes; apodous 4–7 in ♀♀, 5–9 in ♂♂. Apodous segments without supernumerary spines on ventral surface.

Telson.—Median spines large, 1–4, in a single median row (Text-fig. 5B). Furcal spines large, number sometimes varying from side to side of a single animal, and with few scattered spines on lateral face of telson anteriorly.

Posterior marginals small, fine and marginal in the adult, and posterior margin of telson sometimes drawn out to resemble a rudimentary supra-anal plate (Text-fig. 6C).

Furca generally long.

Appendages.—48–57 pairs recorded, but variation probably greater. Endites of first thoracic appendage long.

Sexual dimorphism.—Not as well marked as in other species; no males with furcal scales seen. Abonyi (1926) records two sets of males in one summer in the same pool of which the second batch had very reduced sexual dimorphism—so a dimorphism of males may exist ?

Larvae.—Metanauplius (Text-fig. 13) ; dorsal organ of instar 1 generally round.

Reproduction.—Bisexual and hermaphrodite ; in the northern regions no males occur and such females as have been examined are hermaphrodite. In the South populations are bisexual and in central Europe males occur sporadically. Mathias (1937) reviews occurrence of males.

GEOGRAPHICAL RACES

1. *Triops cancriformis cancriformis* (Bosc)

RANGE. Whole of species range with exception of that occupied by the other two sub-species.

DESCRIPTION. Carina bears 0–10, generally 2–3, small teeth in front of the terminal spine (Text-fig. 15E) and no large samples without specimens showing these spines are known. Furcal spines small (Text-fig. $5B_2$). Dorsal organ round-oval.

Hermaphrodite and bisexual. Chromosome number $2n = 8$.

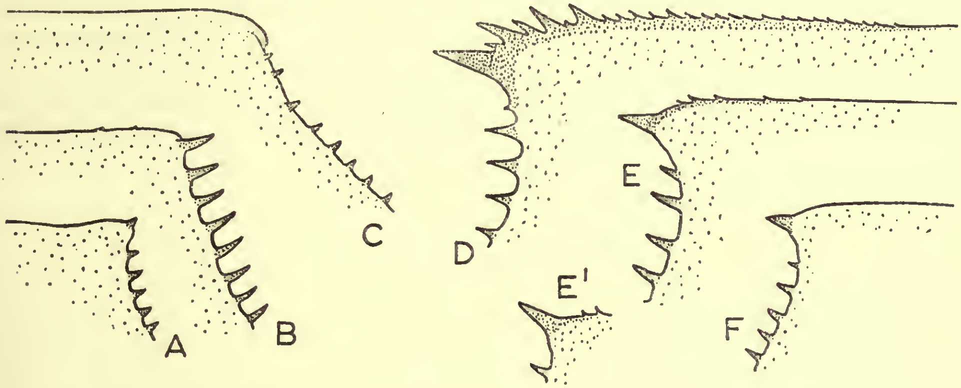

FIG. 15. Carinas of *Triops*. A–C, *T. granarius* ; D, *T. cancriformis mauretanicus* ; E, E_1, *T. c. cancriformis* ; F, *T. cancriformis simplex.*

2. *Triops cancriformis simplex* Ghigi

RANGE. North Africa, Ceuta to Egypt.

DESCRIPTION. Characters of *Thriops simplex* Ghigi. Carina quite smooth in front of the terminal spine (Text-fig. 15F) ; this is invariable in the specimens I have seen from this area, and in those seen by Gauthier (1934), Colosi (1922) and Ghigi (1921). Furcal spines small (Text-fig. $5B_2$). These populations frequently show a tendency to a general weakness in the strength of the armature and include the sample from Kebili (p. 14) which has specimens with no carapace armature whatever. The terminal spine of the carina is frequently reduced.

Apodous segments frequently higher in number than the nominate race (♀♀ 5–7, instead of 4–6).

Bisexual.

3. *Triops cancriformis mauretanicus,* Ghigi

Range. N.W. Africa: French Morocco and Tangier. S. Spain and Balearics (Minorca).

Description. With the characters of *Thriops mauretanicus* Ghigi: armature very strongly developed; carina with a number of teeth posteriorly (Text-fig. 15D), the largest often sub-equal to the terminal spine. Furcal spines very large (Text-fig. 6C); ventral marginal spines on apodous segments very coarse. Apodous number is similar to that of sub-species 2. Dorsal organ oval.

Bisexual.

Synonyms

Apus viridis Bosc was applied to figures of Schaeffer (1756) which showed juvenile *Triops cancriformis; Triops palustris* Schrank is presumably of this species because of its N. European locality; *Apus montagui* Leach, type in BMNH and clearly of this species; *Apus himalayensis* Packard, author's figures show clearly the *cancriformis*-type telson; *Apus varsovianus*, etc. Fiszera, figures similarly show *cancriformis*-type telson; Sidorov's two sub-species are insufficiently described and can both be referred to this species; *Thriops apulius* Ghigi; this could be either sub-species 1 or 2 as it was a single specimen with a smooth carina, but from its Italian locality is probably of sub-species 1.

TRIOPS GRANARIUS (Lucas)

1864. *Apus granarius* Lucas.
1865. *Apus numidicus* Grube.
1877. ? *Apus dispar* Brauer.
1877. *Apus sudanicus* Brauer.
1880. *Apus dukeanus* Day.
1886. *Apus bottegoi* Prato.
1886. *Apus namaquensis* Richters.
1893. *Apus sudanicus* var. *chinensis* Braem.
1893. ? *Apus sudanicus* var. *braueri* Braem.
1893. *Apus numidicus* var. *strauchii* Braem.
1893. *Apus numidicus* var. *dybowskii,* Braem.
1895. *Apus somalicus* Wedenissow.
1899. *Apus bottegoi,* Bouvier.
1899. *Apus trachyaspis* Sars.
1899. *Apus sculleyi* Sars.
1899. *Apus namaquensis* Sars.
1899. *Apus granarius* Sars.
1907. *Apus elongatus* (nom. nov. for *namaquensis* Sars) Thiele.
1920. *Apus zanoni* Colosi.
1921. *Apus asiaticus* (nom. nov. for *granarius* Sars) Gurney.

1922. *Triops ucbensis* (nom. nov. for *bottegoi* Bouvier) Colosi.
1924. *Apus ovamboensis* Barnard.
1927. *Apus numidicus* var. *sinensis* Uéno.
1929. *Apus cancriformis*, Barnard. (non Schaeffer, 1756).
1929. *Apus sudanicus*, Barnard. (? Brauer, 1877.)
1934*a*. *Apus granarius*, Gauthier.
1937. *Apus sudanicus*, Gauthier. (non Brauer 1877).
1939. *Apus numidicus*, Pérès.
1940. *Apus sinensis* Uéno.
1952. *Apus mavliensis* Tiwari.
1952. *Apus orientalis* Tiwari.

TYPE. MNHNP ; ♂ Holotype, unregistered other than label " Type *A. granarius* Lucas ".

RANGE. South Africa to China ; the whole of Africa except for unsuitable forest regions in west and centre ; Middle East, India, central and eastern Asia to the north Chinese coast. Single sample in MNHNP labelled " near Paris " almost certainly mistake in labelling.

HABITAT. Temporary fresh and brackish waters ; unknown from rice fields ; Pérès (1939) compares its distribution in North Africa with that of *Triops cancriformis* and finds latter in steppe zones (300 mm. annual rain) and in the sub-steppe (300–500 mm.) while present species is restricted to the sub-steppe.

DESCRIPTION. Shows great variation in body length and includes very short and long bodied forms with all the associated variation.

Head.—Dorsal organ triangular, oval or round in the short bodied forms, anterior margin between the eyes. Second maxilla present in all specimens examined except in one case (see below).

Carapace.—Shape variable, round to oval. Carina with terminal spine in short bodied forms only (Text-fig. 15), generally smooth. Sulcus round (or squared in some African short bodied forms), spines many, often reduced in size, 24–72.

Body.—Segments : ♀♀, 32–42 ; ♂♂, 32–43. Apodous : ♀♀ 4–13 ; ♂♂, 6–14. Apodous always with varying number of supernumerary spines ventrally (Text-fig. 8B).

Telson.—(Text-fig. 5C$_2$, 6A). Medians small, numerous, scattered, but when low in number may form a rough row medianly, though this never as accurate as in *Triops cancriformis*, and spines smaller. Furcals small and with many scattered in front of them. Posterior marginals small, squat and marginal. Furca variable with body length.

Appendages.—44–46 recorded, but variation probably much greater than this. Endites of first thoracic appendage variable with body length (Text-fig. 2).

Sexual dimorphism.—Strong in many long bodied specimens, males having strong scales on furcal (Text-fig. 8D).

Larvae.—Metanauplius, those seen having in instar 1 a trapezoid-shaped dorsal organ which later changes to triangular.

Reproduction.—Bisexual. Chromosome number $2n = 8$.

Geographical Races

With present knowledge not possible to recognize any with certainty. Some indications known—many South African (not S.W.A.) and Middle East (Bombay-Baghdad) specimens have reduced sexual dimorphism even in long bodied forms; these correspond to *Apus asiaticus* Gurney and this name may eventually be applied to a race with a restricted range. Some specimens from Eastern Asia have reduced second maxilla, and this is even absent in few out of large sample (BMNH 1935. 6.18. 7–12) and these might be separated off as another race, but evidence too weak at present.

Synonyms

Apus sudanicus Brauer belongs here doubtfully as the description is inadequate and I have not seen the types, but Barnard's specimens determined as this are certainly *Triops granarius*. A number of species are placed here on evidence of original descriptions: *A. numidicus* Grube, Braem's varieties of *A. numidicus* and *A. sudanicus* (exc. var. *braueri* which is doubtfully here for it refers to Brauer's description of *A. sudanicus*), *A. somalicus* Wedenissow, Sars' three species (1899), *A. granarius* Sars and the nom. nov. *asiaticus* Gurney, Uéno's var. *sinensis* and *A. sinensis*. I have seen the types of *A. granarius* Lucas, *A. bottegoi*, Bouvier, *Apus ovamboensis* (= *cancriformis* sens Barnard), and of Tiwari's two species. *A. mavliensis* Tiwari, in spite of its odd appearance is clearly only a young form of this species. *A. bottegoi* Prato is insufficiently described and may belong here or to the previous species.

TRIOPS LONGICAUDATUS (LeConte)

1846. *Apus longicaudatus* LeConte.
1852. *Apus domingensis* Baird.
1871. *Apus aequalis* Packard.
1871. *Apus lucasanus* Packard.
1871. *Apus newberryi* Packard.
1907. *Apus frenzeli* Thiele.
1916. *Lepidurus patagonicus*, Bruch. (non Berg, 1900).
1944. *Triops pampaneus* Ringuelet.
1947. *Apus biggsi* Rosenberg.
1947. *Apus oryzaphagus* Rosenberg.
1952. *Apus longicaudatus*, Linder.

Range. Western North America, south of 50° N, through Central to South America, where only very scattered records (Thiele, 1907; Bruch, 1916; Ringuelet, 1944; Linder, 1952). W. Indies, Galapagos Islands, Hawaii, Japan and New Caledonia.

Habitat. Temporary fresh waters, rice fields in California and Japan.

Description. As variable as the preceding species, but not so many short bodied forms seen.

Head.—Dorsal organ usually triangular, round in short bodied forms, and anterior margin between the eyes. Second maxilla absent in all the specimens seen.

Carapace.—Text-fig. 2G., H). Shape varies from oval to round with segment number. Terminal spine of carina very small when present, but generally absent. Carina finely denticulate along whole length in some specimens. Sulcus tends to be broad and shallow, spines variable in size, 24–60.

Body.—Segments : ♀♀, 35–43 ; ♂♂, 35–44. Apodous segments : ♀♀, 5–12 ; ♂♂, 10–13 in material examined. Apodous segments with varying number of supernumerary spines on ventral surface.

Telson.—(Text-fig. 5 D_2.) Medians large, 1–3, in a single row in the midline. Furcal spines smaller than those of *T. cancriformis*. Posterior marginals very large, set in the adult well forward of the margin, often pointing vertically. This arrangement of marginals unique and all specimens of this species have it.

Appendages.—54–66. (Linder's data mainly) : endites of first thoracic appendage variable with segment number.

Sexual dimorphism.—Well marked in specimens with high segment numbers, males then having furcal scales.

Larvae.—Metanauplius, indistinguishable from that of *T. granarius*.

Reproduction.—Bisexual and hermaphrodite, the latter only in California and Pacific region populations.

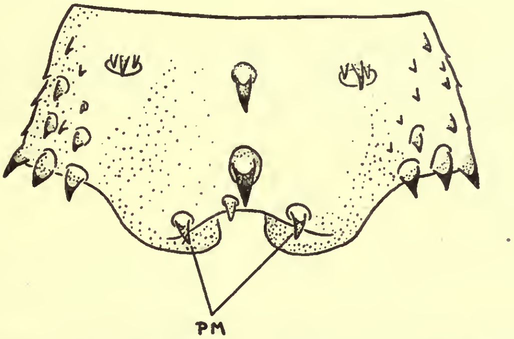

FIG. 16. Telson of *Triops longicaudatus intermedius*. (*pm* = posterior marginals).

GEOGRAPHICAL RACES

1. *Triops longicaudatus longicaudatus* (LeConte)

RANGE. That of species with exception of New Caledonia.

DESCRIPTION. With the characters described above. There may be a difference in the shape of the posterior margin of the telson on the forms from Galapagos and Hawaii as against continental American forms ; in the former the posterior margin is quite straight with no trace of an emargination in many specimens. This may well be evidence for a sub-species inhabiting these islands. Chromosome number $2n = 8$.

2. *Triops longicaudatus intermedius* subsp. n.

RANGE. New Caledonia. Two samples in MNHNP labelled " 93–1887 " and

" coll. Simon 25–96 " respectively are of this form and no others from the island are known to me. These specimens, all females, form the paratypes of the new subspecies. The name suggests that in their telson armature they are intermediate in form between their nominate race and the rest of the genus.

DESCRIPTION. Second maxilla absent, segments 39, apodous 8–9. Dorsal organ small, triangular to round. Carapace oval, terminal spine of carina very reduced, sulcus spines long, 24–30. Few supernumerary spines on apodous segments ventrally. Telson : medians large, 2–3, in mid-line, posterior marginals much smaller than in nominate race but well forward of the margin (Text-fig. 16). This is the most characteristic feature.

SYNONYMS

Apus obtusus James, 1823 and *Apus guildingi* Thompson, 1834 are clearly of this species on geographical grounds, but neither description is detailed enough to confirm this. Linder has shown that Packard's and Rosenberg's species are synonyms of this species. The diagrams of *A. frenzeli* and *Triops pampaneus* both show the *longicaudatus*-type telson, and Bruch's record of *Lepidurus patagonicus* is accompanied by a figure which certainly shows a *Triops*, and probably *T. longicaudatus*, though the telson is not very clear.

TRIOPS AUSTRALIENSIS (Spencer and Hall)

1896. *Apus australiensis* Spencer and Hall.
1905. *Apus sakalavus* Nobili.
1907. *Apus madagassicus* Thiele.
1911. *Triops gracilis* Wolf.
1911. *Triops strenuus* Wolf.

RANGE. The drier regions of Australia, where it may be locally very common. Madagascar.

HABITAT. Temporary fresh water, sometimes (Wolf, 1911 ; Main, 1953) in saline or alkaline pools and lakes.

DESCRIPTION. Includes extremes of long and short bodied forms ; from Australia several samples have been seen with aberrations (not damage) to limbs and lobes of limbs ; both females in a sample from Ayer's Rock have reduced 11th thoracic appendages so that these are but a stump with a duct running through it on one side of each specimen. Several samples from W. Australia have endites 5 and 6 reduced to rudiments on one side of the thoracic series.

Head.—Dorsal organ triangular, ovoid or " wide ", often set with the anterior margin well behind the eyes (Text-fig. 4B). Second maxilla absent in all specimens seen.

Carapace.—Shape variable, terminal carinal spine usually absent and carina frequently denticulate along the whole length. Sulcus round, often small, spines variable in size, and numerous, 28–62.

Body.—Segments : ♀♀, 35–43 ; ♂♂, 36–44. Apodous : ♀♀, 5–12 ; ♂♂, 9–13. Apodous segments with varying number of supernumerary spines ventrally.

Telson.—Medians small, scattered, fewer than in *T. granarius*, often very few or even absent (Text-fig. 6B); furcal spines small, posterior marginals small, squat and marginal in the adult. Furca varies with the segment number.

Appendages.—48–66, but only few specimens counted. Endites variable with segment number.

Sexual dimorphism.—As in previous two species.

Larvae.—Metanauplius, indistinguishable from that of *T. granarius*.

Reproduction.—Bisexual.

Geographical Races

1. ***Triops australiensis australiensis*** (Spencer and Hall)

RANGE. Continental Australia.

DESCRIPTION. With the characters described above. Chromosome number $2n = 10$.

2. ***Triops australiensis sakalavus*** (Nobili)

RANGE. Madagascar.

DESCRIPTION. Very similar to the nominate race, but median spines are rather more numerous in the specimens I have seen in MNHNP, which otherwise are clearly of this species, and not of *T. granarius*; the specimens have no second maxillae, the carinae are denticulate, and the median spines are relatively sparse compared with *T. granarius*.

Synonyms

Wolf's species are clearly *Triops australiensis*, showing the typical telson pattern and Main has already (1953) suggested uniting them with it. *T. madagassicus* and *T. sakalavus* are placed here on the assumption that only one species will occur in Madagascar, since sympatric species are the exception in the Notostraca, but future work will be needed to confirm this arrangement.

Genus ***LEPIDURUS*** Leach

1756. *Apus* Schaeffer (in part).
1758. *Monoculus* Linn. (in part).
1819. *Lepidurus* Leach.
1924. *Bilobus* Sidorov.

Distinguished at once from *Triops* by the presence of a supra-anal plate. In general, also, the segment number is lower, the carapace is longer and more compressed laterally, the sexual dimorphism is weaker than in the other genus.

Bilobus Sidorov was erected on the erroneous assumption that median incision of the posterior margin of the supra-anal plate was important systematically (see p. 22, and Linder, 1952).

LEPIDURUS APUS (Linn.)

1756. *Apus cancriformis* Schaeffer (in part).
1758. *Monoculus apus* Linn. (in part).
1801. *Apus productus* Bosc.
1819. *Lepidurus productus* Leach.
1850. *Lepidurus viridis* Baird.
1866. *Lepidurus angasi* Baird.
1873. *Lepidurus lubbocki* Brauer.
1875. *Lepidurus couessii* Packard.
1877. *Lepidurus macrourus* Lilljeborg.
1879. *Lepidurus viridulus* Tate.
1879. *Lepidurus kirki* Thompson.
1879. *Lepidurus compressus* Thompson.
1886. *Lepidurus packardi* Simon.
1893. *Apus extensus* Braem.
1900. *Lepidurus patagonicus* Berg.
1909. *Lepidurus apus* Keilhack.
1911. *Lepidurus hatcheri* Ortmann.
1921. *Lepidurus barcaeus* Ghigi.
1952. *Lepidurus couessii,* Linder.

RANGE. Europe (excluding Britain), North Africa, Palestine, Asia Minor, Russia ; North and South America ; New Zealand and Australia.

HABITAT. Temporary fresh waters, but perhaps less restricted to those which regularly dry out than, for instance, *Triops cancriformis.* Occurs in alkaline pools in North America.

DESCRIPTION. This species has the largest range of any known Notostracan and shows very little variation over the whole area.

Head.—Dorsal organ round or oval (Text-fig. 4E, F), anterior margin between the eyes with the possible exception of the specimens seen by Ortmann (1911) from Patagonia. Second maxilla present in all the specimens seen by me.

Carapace.—Oval, fairly compressed laterally but not so markedly as in next species. Terminal spine of carina only rarely absent. Sulcus spines usually long, rarely (*packardi*) reduced. Normally 35–50 in number.

Body.—Segments, 26–29 ; Apodous, 4–6. No supernumerary spines on apodous segments.

Telson.—Supra-anal plate relatively longer than in next species, the ratio carapace/supra-anal plate being about 4–6 in adults. The marginal spines of the plate are small and numerous in all except the South American forms. Central spines 4–100 or more, the higher numbers being borne on a distinct keel (Text-fig. 7A).

Appendages.—35–48 ; endites of first thoracic appendages reach to the end of the carapace in some, in others little longer than *L. arcticus.*

Sexual dimorphism.—Males occur, and the supra-anal plate is longer and more spatulate in these ; otherwise the dimorphism is weak.

Larvae.—Metanauplius in the European and New Zealand forms and probably in all. May differ from that of Triôps by presence of rudiments of paired eyes in the first instar (Bernard, 1892 : 158).

Reproduction.—Bisexual and hermaphrodite.

GEOGRAPHICAL RACES

1. *Lepidurus apus apus* (Linn.)

RANGE. Europe (exc. range of next ssp.), Asia, North America (exc. California).

DESCRIPTION. Segments, 26–28; apodous, 4–5; supra-anal plate with 20–100 spines generally borne on a keel; marginal spines of plate fine and numerous. Bisexual and hermaphrodite.

2. *Lepidurus apus lubbocki* Brauer

RANGE. N. Africa, Palestine, Syria, Italy, Sicily.

DESCRIPTION. Segments, 27–29; apodous, 5–6; supra-anal plate (Text-fig. 7B) with fewer central and marginal spines than above ssp (3–20 centrals) and keel less prominent. Specimens from eastern part of the range tend to have the fewest central spines; endites relatively longer than nominate race. Bisexual. Chromosome number, $2n = 12$ (Goldschmidt).

3. *Lepidurus apus packardi* Simon

RANGE. California.

DESCRIPTION. Segments and supra-anal plate similar to sub-species 2. Sulcus differs from that of all other forms by having very many small spines forming a granulated margin. Bisexual.

4. *Lepidurus apus patagonicus* Berg

RANGE. South America (Chubut Territory, Patagonia).

DESCRIPTION. Segments, 29; apodous, 5. Marginal spines of supra-anal plate coarser and fewer than previous forms, central spines few. Sulcus spines as typical race. Bisexual.

5. *Lepidurus apus viridis* Baird

RANGE. New Zealand, Tasmania, and coastal or better watered regions of Australia.

DESCRIPTION.—Very similar to nominate race. Segments, 27–28; apodous, 4–5. Generally with low number of central spines on the plate (5–10), but one specimen from Tasmania had more than 20; average is much lower than in nominate race, however. I have seen no males.

SYNONYMS

I have examined the following types, and am satisfied that they are correctly placed here: *L. packardi*, *L. extensus*, *L. barcaeus*, *L. angasi*, *L. compressus*, *L. kirki*, *L. viridulus*. The rest are included on the basis of the original descriptions or on material previously determined.

Lepidurus lemmoni (Holmes, 1894). Holmes' description does not enable determination of his specimens with any here recognized, yet contains nothing to indicate good differences from them; the types are lost (Linder, 1952), and therefore it is advisable to abandon the species.

LEPIDURUS ARCTICUS (Pallas)

1793. *Monoculus arcticus* Pallas.
1883. *Lepidurus glacialis* Packard.
1892. *Lepidurus spitzbergensis* Bernard.
1893. *Apus productus* var. *glacialis* Braem.
1896. *Lepidurus glacialis*, Sars.
1927. *Lepidurus ussuriensis* Sidorov.

RANGE. Circum-polar Arctic regions; Aleutians, North America; Alaska to Labrador, Greenland, Iceland, Bear Island, Spitzbergen, Northern Palaearctic; Scandinavia to Siberia.

HABITAT. Temporary fresh-water pools, the streams connecting pool systems, and large lakes which are permanent. A reservoir in the Norwegian mountains (Sømme, 1934).

DESCRIPTION. *Head.*—Dorsal organ oval, sometimes very elongated, anterior margin just between the eyes (Text-fig. 4G). Second maxilla present.

Carapace.—Oval, laterally very compressed. Terminal carina spine present, long. Rest of carina smooth.

Body.—Segments, 26–28; apodous, 4–5. Apodous without supernumerary spines on ventral surface.

Appendages.—41–46, but variation probably greater. Endites of the first thoracic appendage very short, scarcely reaching beyond margin of carapace (Text-fig. 10A).

Telson.—Supra-anal plate very small; carapace/plate = about 12 in adults of 20 mm. carapace length. Median spines very sparse (0–5) and marginals few and coarse (Text-fig. 7C).

Sexual dimorphism.—Males rare, but known to have longer and more spatulate supra-anal plates.

Larvae.—Post-metanauplius (Poulsen, 1940, and my cultures), equivalent to about instar 3 of *Triops* larvae (Text-fig. 13).

Reproduction.—Bisexual and hermaphrodite. Males known from Bear Island in very low proportion of the population. (Sømme, 1934).

GEOGRAPHICAL RACES

None could be recognized in the material available, nor could Linder (1952) find any subdivisions of his material. *Lepidurus ussuriensis* Sidorov appears to be of this species, for the endites are shorter than is usual in other species, and the supra-anal plate is small (carapace/plate = about 9) and typical of this species in its armature. However, the endites are projecting more beyond the carapace than is usual in *L. arcticus* and may indicate a difference between this East Siberian form and the typical Arctic forms. The weakness of the carina and the elongate form of the dorsal organ confirm the placing of this species in *L. arcticus*.

LEPIDURUS BILOBATUS Packard

1883. *Lepidurus bilobatus* Packard.
1952. *Lepidurus bilobatus*, Linder.

RANGE. North America ; Utah, Colorado, probably Arizona (Linder, 1952).

HABITAT. Not known, but occurs in arid areas so presumably in temporary pools and lakes.

DESCRIPTION. Known only from Packard's description, and two further specimens ascribed to the species by Linder.

Head.—Dorsal organ round or oval, anterior margin set between the eyes.

Carapace.—Arrangement of sulcus spines normal.

Body.—Segments, 33 ; apodous, 6.

Telson.—Supra-anal plate with numerous small marginals, 4–6 centrals.

Appendages.—60 ; endites of first thoracic appendage as in *Lepidurus apus.*

Sexual dimorphism.—Males unknown.

Larvae, Reproduction.—Unknown.

LEPIDURUS LYNCHI Linder

1952. *Lepidurus lynchi* Linder.
1952. *Lepidurus lynchi* var. *echinatus* Linder.

TYPES. Holotype (♀) and allotype (♂) in Uppsala Museum ; paratypes USNM 82101 ; var. *echinatus.* Holotype (♀) USNM 82068, allotype (♂) USNM 82069.

RANGE. North America ; Washington, Nevada, and Oregon.

HABITAT. Apparently in lakes (Linder, 1952 . . . North end of Goose Lake in water two feet deep, muddy), but probably also in temporary pools.

DESCRIPTION. Long bodied form with unique carapace armature.

Head.—Dorsal organ round with the anterior margin set well behind the eye tubercles.

Carapace (Text-fig. 3).—Oval. Carina absent except when it bears series of unusually large spines. Specimens from first two localities have 0–20 of these carinal spines. Some of those from Oregon have series of large spines along posterior part of lateral margin in addition to carinal spines and carapace shape may be more round in these. But no useful purpose is served by the formal term var. *echinatus* for these latter forms ; *L. lynchi* is obviously characterized by the possession of large spines on carina and margin and there is much variation in the distribution of these spines ; even in the specimens from the first two localities the margin of the carapace bears larger spines than is usual in *Lepidurus.*

Body.—Segments, 31–34 ; apodous, 3–5.

Telson.—Supra-anal plate about same size as in *L. apus,* central spines 2–7, marginals very large and sparse.

Appendages.—60–71. Endites as in *L. apus.*

Sexual dimorphism.—Normal for the genus.

Reproduction.—Bisexual.

LEPIDURUS BATESONI sp. nov.

TYPES. Holotype (♂) and two paratypes in BMNH (1911.11.8, 23542–4, Norman collection). Collected by W. Bateson.

RANGE. Russia. Probably collected at Chilik Kul in the Kazak region, where Bateson made a collection of other fresh-water entomostraca also in the Norman collection.

DESCRIPTION. Males only known. Long bodied form in general appearance (Text-fig. 2J).

Head.—Eyes and dorsal organ similar to those of *Lepidurus lynchi*. Second maxilla present and typical of the genus.

Carapace (Text-fig. 2J). Oval-round, more rounded than in *Lepidurus apus*. Carina and its terminal spine absent in all specimens seen ; position of carina demarcated only by the light streak of the dorsal blood channel of the carapace which follows the line of the carina in normal forms. Sulcus wide, rounded, with small sulcal teeth.

Body.—Segments 33, apodous 8, in all. Apodous ventral marginal spines very small and widely separated centrally, no supernumeraries.

Appendages.—49–52. Endites of first thoracic appendage (Text-fig. 10D) unique in known Notostraca ; endites 4 and 5 very short ; much more reduced than in *Lepidurus arcticus* and can scarcely have projected beyond carapace margin in life ; endite 5 of this appendage is little more developed than endite 5 of the second appendage. Endite 6 of the first appendage is fully developed and claw-like as in the subsequent appendages (in all other Notostraca the 6th endite of the first thoracic appendage is reduced to a small soft lobe at the base of the 5th endite).

Telson (Text-fig. 7B).—Supra-anal plate very similar to that of *Lepidurus lynchi*, central spines few (4), marginals few, coarse.

Sexual dimorphism.—Females unknown.

Reproduction.—Bisexual.

Note.—One of the paratypes has an abnormality of the supra-anal plate, which is reduced in size, soft, and lacks its armature.

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THE POLYCHAETE FAUNA OF THE GOLD COAST

NORMAN TEBBLE

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ZOOLOGY Vol. 3 No. 2
LONDON: 1955

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BY

NORMAN TEBBLE

Pp. 59–148 ; 1 *Chart* ; 30 *Text-figures*

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THE POLYCHAETE FAUNA OF THE GOLD COAST

By NORMAN TEBBLE

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1. INTRODUCTION

No large collections of Polychaetes from the Gold Coast have previously been systematically studied, though a few records were noted by Augener (1918). The present Faunal Survey results from the examination of littoral collections, down to a depth of 51 metres, made by Mr. R. Bassindale in 1949–51. Important additional material has been collected by Mr. J. B. Buchanan. The author is grateful to these gentlemen for the privilege of studying these collections, through which the known geographical distribution of many species is extended. Altogether ninety-five records of Polychaetes from the Gold Coast are here reported, including two new to science.

In the Systematic Section a key to all families, keys to genera and species where necessary and a glossary of terms used in the descriptions have been included. All previous records from the area have been noted although they may refer to species not examined here. References to species have been restricted, as far as possible, to standard monographic studies on the group; the most important are Augener, 1918, and Fauvel, 1923 and 1927*a*.

Dr. A. B. Hastings kindly identified the Polyzoan specimens with which some Serpulidae are associated and the author also wishes to acknowledge the technical assistance he has received from Miss A. C. Edwards, of the British Museum (Nat. Hist.) staff, particularly in the drawing of figures and charts.

2. STATION DETAILS

Littoral collections were made at the following places; the details have been provided by Mr. R. Bassindale.

I. *Accra* (5° 30′ N., 0° 15′ W.) (*a*) Christiansborg. The reef at Christiansborg lies at the foot of the Governor's Castle (2 miles east of Accra lighthouse) and consists of native rock with small deep pools mainly at the lowest levels. There is sand and just a little exposed rock above mid-tide level.

(*b*) Chorkor. A seine net was operated from the sand beach here, two miles west of Accra lighthouse.

II. *Tenpobo and Pram Pram*, 24 and 23 miles, respectively, east of Accra. The coast is of sand and the upper three-quarters of the beach is a steep sand slope. Near the headlands of a series of shallow bays there are low level rocks and boulder reefs jutting out to sea. These reefs occupy the lowest foot of spring tide range except for native rock, which may rise one or two feet above this level. Maximum tidal range is six feet, and neap tides do not expose the levels from 0–1 foot above chart datum (low tide level of ordinary spring tides). At Tenpobo the reefs are protected from low level wave wash by a line of high rocks to seaward. There are many small boulders and stones on the reef ; gravel and sand packing between the stones is common.

III. *Winneba*, 32 miles west of Accra. The beach here is of native rock from below low tide level to above high tide level.

IV. *Apam*, 39 miles west of Accra. The shore is of rock and boulders set in sand with rock pools. Extending to the east is a shallow sand bay with sandy mud in the shelter of the Apam headland.

V. *Sekondi*, 113 miles west of Accra. Collections here were made from the horizontal surface of a rock plateau at or above high tide level. The waves wash over the plateau at most states of the tide and so replenish the pools. There is probably no period of complete submergence of the plateau.

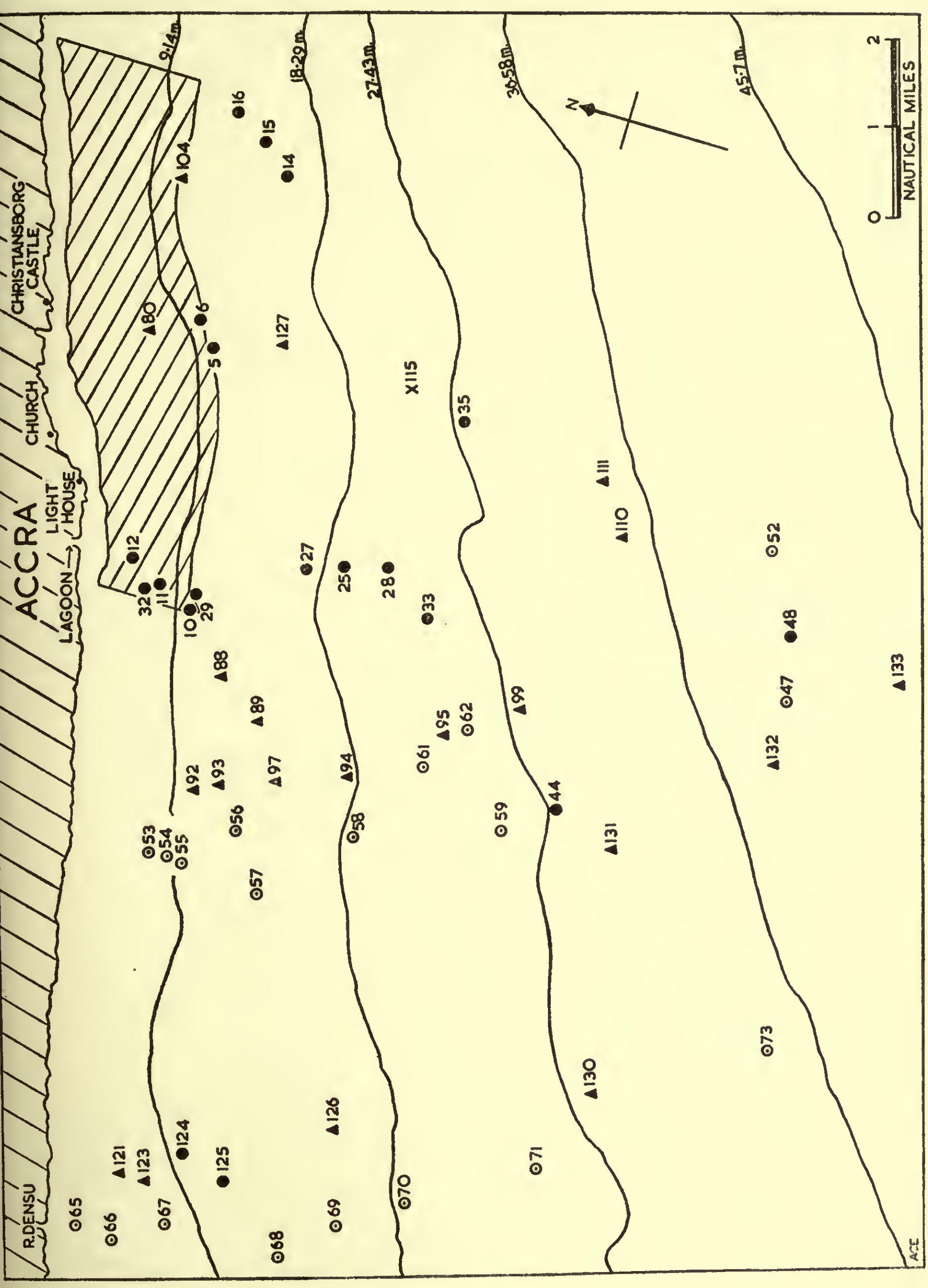
VI. *Dixcove*, 131 miles west of Accra. The bay at Dixcove is almost square, the sides being about 400 yards long. The innermost side of the bay has a sandy beach with large boulders and native rock at low tide level—the rocks rising to mid-tide level or higher. Collections were also made on the western side of the bay which consists of small boulders and stones, with sand, mud and gravel closer in.

VII. *Princes Town*, 142 miles west of Accra. A solid rocky headland very much wave-washed, with a few boulders round the headland to the east.

VIII. *Axim*, 154 miles west of Accra : (*a*) The Hospital Reef consists of a narrow belt of rock, boulders and stones jutting out to sea. Collections here were made from the exposed side.

(*b*) The Lighthouse Reef juts out in a similar way but is protected by two islands, one half way along and one at the seaward end. In-shore the reef is at low level and has stones with gravel, sand and mud. Further out the stones increase in size until very large boulders occur on the exposed side. Collections here were made mainly from the sheltered side.

Off-shore collections were made by Mr. Bassindale entirely within the area off Accra shown on the chart (p. 63). The following lists give further details of the stations. Several collections were made by Mr. Bassindale at stations which are not


ACCRA
R. DENSU
LAGOON
LIGHT HOUSE
CHURCH
CHRISTIANSBORG CASTLE
9·14m.
18·29m.
27·43m.
36·58m.
45·7m.
N
0
1
2
NAUTICAL MILES
5
6
10
11
12
14
15
16
25
27
28
29
32
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130
131
132
133
▲ AGASSIZ TRAWL.
x OTHER STATIONS.
● LARGE DREDGE.
▨ BUCHANAN SURVEY
⊙ SMALL DREDGE.
3·6 to 11·0 METRES.

CHART OF STATIONS
IN THE SEA OFF ACCRA.

numbered and they are referred to in the text by reference to points on the coast. Mr. Buchanan made part of his survey within the area indicated on the chart between 3·6 and 11·0 metres; other stations at which he made collections have also been referred to as the Buchanan Survey and their positions have been indicated in the same way.

List of Collecting Stations in the Sea off Accra

All dredge hauls of 10 minute duration and Agassiz Trawl hauls of 15 minute duration except where stated.

Station number	Date	Depth in metres	Instrument used	
5	9.xi.50	13	Large dredge	
6	,,	12	,,	
10	19.xi.50	14	,,	9 min.
11	,,	13	,,	
12	,,	16	,,	
14	28.xi.50	20	,,	
15	,,	16	,,	
16	,,	17	,,	
27	14.xii.50	22	,,	5 min.
28	,,	30	,,	8 min.
29	20.xii.50	13	,,	
32	,,	11	,,	
33	,,	28	,,	
35	21.xii.50	37	,,	30 min.
44	31.xii.50	35	,,	
47	4.i.51	44	Small dredge	15 min.
48	,,	44	Large dredge	
52	,,	45	Small dredge	
53	15.i.51	11	,,	
54	,,	11	,,	
55	,,	12	,,	
56	,,	16	,,	
57	17.i.51	16	,,	
58	,,	20	,,	
59	,,	24	,,	
61	18.i.51	26	,,	
62	,,	30	,,	
65	22.i.51	7	,,	
66	,,	10	,,	
67	,,	14	,,	
68	,,	19	,,	
69	,,	22	,,	
70	24.i.51	25	,,	
71	,,	30	,,	
73	,,	41	,,	
80	21.ii.51	10	Agassiz Trawl	
88	5.iii.51	13	,,	
89	7.iii.51	16	,,	

List of Collecting Stations in the Sea off Accra—cont.

Station number	Date	Depth in metres	Instrument used	
92	12.iii.51	11	Agassiz Trawl	
93	,,	12	,,	
94	,,	17	,,	
95	,,	17	,,	30 min.
97	14.iii.51	20	,,	
99	,,	28	,,	
104	29.iii.51	13	,,	
110	4.iv.51	40	,,	20 min.
111	,,	43	,,	
115	5.iv.51	24	No details	
121	11.iv.51	8	Agassiz Trawl	
123	,,	9	,,	
124	12.iv.51	11	,,	
125	,,	16	,,	
126	,,	20	,,	
127	14.iv.51	17	,,	
130	26.iv.51	32	,,	
131	2.v.51	37	,,	
132	,,	44	,,	
133	,,	51	,,	

Approximate distance covered in normal 10-minute haul with large dredge was 700 metres, in normal 15-minute haul with Agassiz Trawl, 400 metres. (More in shallow and less in deep water.)

3. LIST OF SPECIES AND DISTRIBUTION

× = Collected in the present survey.
o = Recorded by Augener (1918), not collected in the present survey.

	Localities										
		Accra							Axim		
Species	Tenpobo and Pram Pram	Intertidal	Off-shore	Winneba	Apam	Sekondi	Dixcove	Princes Town	Hospital Reef	Lighthouse ,,	Shore
APHRODITIDAE											
Aphrodite alta	..	..	×	..	..	..	..	..	..	..	..
Hermione hystrix	..	..	×	..	..	..	..	..	..	..	..
Panthalis bicolor	..	..	×	..	..	..	..	..	..	..	..
Euthalenessa insignis	..	..	..	..	o	..	..	..	..	..	..
Eusigalion vazensis	..	..	×	..	..	..	..	..	..	..	..
Sthenelais boa	×	..	..	..	..	..	..	..	..	..	..
,, *limicola*	..	..	×	..	..	..	..	..	..	..	
Leanira japonica	..	..	×	..	..	..	..	..	..	..	..
,, *yhleni*	..	..	×	..	..	..	..	..	..	..	..

List of Species and Distribution—cont.

× = Collected in the present survey.
o = Recorded by Augener (1918), not collected in the present survey.

Species	Localities										
	Tenpobo and Pram Pram	Accra		Winneba	Apam	Sekondi	Dixcove	Princes Town	Axim		
		Intertidal	Off-shore						Hospital Reef	Lighthouse ,,	Shore
Scalisetosus pellucidus	..	..	×	..	..	..	..	..	..	..	..
Acholoë astericola	..	..	×	..	..	..	..	..	..	..	..
Pareulepis geayi	..	..	×	..	..	..	..	..	..	..	..
Lepidonotus hupferi	×	..	×	..	..	..	..	..	×	..	×
Harmothoë goreensis	..	..	×	..	..	..	..	..	..	..	..
CHRYSOPETALIDAE											
Bhawania goodei	o	×	..	..	..	..	..	..	×	..	..
AMPHINOMIDAE											
Chloeia viridis	..	..	×	..	..	..	..	..	..	..	..
Hermodice carunculata var *didymobranchiata*	..	..	×	..	..	..	..	..	..	..	..
Eurythoë complanata	×	..	..	..	..	..	×	..	×	..	×
,, *parvecarunculata*	..	..	×	..	..	..	..	..	..	..	..
PHYLLODOCIDAE											
Phyllodoce africana	..	..	×	..	..	..	..	..	..	..	..
,, *oculata*	..	..	o	..	..	..	..	..	..	..	..
Eteone picta	..	..	×	..	..	..	..	..	..	..	..
HESIONIDAE											
Leocrates claparedii	..	..	..	..	..	..	..	..	×	..	..
SYLLIDAE											
Trypanosyllis prampramensis	o	..	..	..	..	..	..	..	..	..	..
Syllis gracilis	..	..	×	..	..	..	..	..	..	..	..
,, *variegata*	..	..	..	..	..	..	..	..	×	..	×
,, *hyalina*	o	..	..	..	..	..	..	..	..	..	..
,, *cornuta*	o	..	×	..	..	..	..	..	..	..	×
Opisthosyllis brunnea	×	..	..	×	..	..	..	..	×	..	..
Pionosyllis ehlersiaeformis	..	..	×	..	..	..	..	..	..	..	..
Exogene gemmifera	o	..	..	..	..	..	..	..	..	..	..
NEREIDAE											
Nereis falsa	×	×	×	×	..	..	..	..	×	×	×
Neanthes succinea	..	..	×	..	..	..	..	..	..	..	..
Perinereis melanocephala	×	×	..	×	..	×	×	..	..	..	×
Pseudonereis gallapagensis	..	..	..	×	..	..	..	..	×	..	×

List of Species and Distribution—cont.

× = Collected in the present survey.
o = Recorded by Augener (1918), not collected in the present survey.

Species	Localities										
	Tenpobo and Pram Pram	Accra		Winneba	Apam	Sekondi	Dixcove	Princes Town	Axim		
		Intertidal	Off-Shore						Hospital Reef	Lighthouse ,,	Shore
NEPHTHYDIDAE											
Nephthys hombergii	..	..	×	..	..	..	..	..	..	..	..
Aglaophamus lyrochaetus	..	..	×	..	..	..	..	..	..	..	..
GLYCERIDAE											
Glycera convoluta	..	..	×	..	×	..	..	..	..	..	..
Goniada multidentata	..	..	×	..	..	..	..	..	..	..	..
Goniadopsis incerta	..	..	..	..	×	..	..	..	..	..	..
Ophioglycera archeri sp. n.	..	..	×	..	..	..	..	..	..	..	..
EUNICIDAE											
Eunice antennata	×	..	×	..	..	..	..	..	..	..	..
,, *vittata*	×	..	×	..	..	..	..	..	..	..	..
,, *filamentosa*	..	..	..	..	..	..	..	..	×	..	×
,, *coccinea*	..	..	..	..	..	..	..	..	×	..	..
,, *gracilis*	..	×	×	..	..	..	×	..	×	×	×
,, *rubra*	o	..	..	..	..	..	..	..	..	..	..
Marphysa dartevellei	×	×	..	..	..	..	..	..	×	..	×
Lysidice ninetta	..	..	×	..	..	..	..	..	..	..	..
,, *collaris*	..	..	×	..	..	..	..	..	..	..	..
Diopatra musseraensis	..	..	×	×	..	..	..	..	..	..	..
,, *neapolitana*	..	..	×	..	..	..	..	..	..	..	..
Onuphis eremita	×	..	×	..	..	..	..	..	..	..	..
Lumbrineris impatiens	×	×	..	..	..	..	..	..	..	..	..
,, *albifrons*	..	..	×	..	..	..	..	..	..	..	..
Halla parthenopeia	..	..	×	..	..	..	..	..	..	..	..
ORBINIIDAE											
Orbinia foetida var *linguistica*	..	..	×	..	..	..	..	..	..	..	..
Scoloplos madagascarensis	..	..	×	..	..	..	..	..	..	..	..
,, *dubia*, sp. n.	..	..	×	..	..	..	..	..	..	..	..
SPIONIDAE											
Prionospio pinnata	..	..	×	..	..	..	..	..	..	..	..
CIRRATULIDAE											
Audouinia tentaculata	..	..	..	×	..	..	..	..	..	..	..
,, *filigera*	..	..	..	..	..	×	×	×	×	..	..
,, *punctata*	×	..	..	..	..	..	..	..	..	..	..
Cirratulus filiformis	..	..	×	..	..	..	..	..	..	..	..

List of Species and Distribution—cont.

× = Collected in the present survey
o = Recorded by Augener (1918), not collected in the present survey.

Localities

Species	Tenpobo and Pram Pram	Accra		Winneba	Apam	Sekondi	Dixcove	Princes Town	Axim		
		Intertidal	Off-shore						Hospital Reef	Lighthouse ,,	Shore
FLABELLIGERIDAE											
Stylarioides scutigeroides	..	..	×	..	..	..	..	..	..	..	..
,, *arenosus*			Augener (1918), from Saltpond.								
,, *tropicus*	..	..	o	..	..	..	..	..	..	..	..
OPHELIIDAE											
Armandia intermedia	..	..	×	..	..	..	..	..	..	..	..
Polyophthalmus pictus	×	..	..	..	..	..	..	..	..	×	..
MALDANIDAE											
Maldane sarsi	..	..	×	..	..	..	..	..	..	..	..
OWENIIDAE											
Owenia fusiformis	..	..	×	..	..	..	..	..	..	..	..
SABELLARIIDAE											
Sabellaria eupomatoides	..	×	..	×	×	..	..	..	..	..	..
,, *spinulosa* var *intoshi*	×	..	..	..	×	..	×	..	..	×	..
,, *spinulosa* var *alcocki*	..	..	..	..	..	..	..	..	×	..	..
STERNASPIDAE											
Sternaspis scutata var *africana*	..	..	×	..	..	..	..	..	..	..	..
AMPHARETIDAE											
Phyllamphicteis collaribranchis	..	..	×	..	..	..	..	..	..	..	..
Pterolysippe bipennata	..	..	×	..	..	..	..	..	..	..	..
Isolda whydahensis	..	..	×	..	..	..	..	..	..	..	..
TEREBELLIDAE											
Pista grubei	..	..	×	..	..	..	..	..	..	..	..
Terebellides stroemi	..	..	×	..	..	..	..	..	..	..	..
Streblosoma persica	×	..	..	..	×	..	×	..	..	..	×
Loimia medusa	..	..	×	..	..	..	..	..	..	..	..
Amaea accraënsis	..	o	..	..	..	..	..	..	..	..	..
SABELLIDAE											
Laonome puncturata	..	×	..	..	×	..	..	..	..	..	×
Dasychone lucullana	..	..	×	..	..	..	..	..	..	..	..
Potamilla casamancensis	..	..	×	..	..	..	..	..	..	..	..

List of Species and Distribution—cont.

× = Collected in the present survey
o = Recorded by Augener (1918), not collected in the present survey.

Species	Localities										
		Accra							Axim		
	Tenpobo and Pram Pram	Intertidal	Off-shore	Winneba	Apam	Sekondi	Dixcove	Princes Town	Hospital Reef	Lighthouse ,,	Shore
SERPULIDAE											
Salmacina incrustans	×	..	..	×	×	..	..	..	×	..	..
Hydroides norvegica	..	..	..	..	..	..	..	..	..	..	..
,, *spinosus*	×	..	×	..	..	..	..	..	..	..	..
,, *arnoldi*	..	..	..	..	..	..	..	..	..	..	×
Apomatus similis	..	..	×	..	..	..	..	..	..	..	..
Serpula vermicularis	×	..	×	..	..	..	..	..	..	..	..
Vermiliopsis multicristata	..	..	×	..	..	..	..	..	..	..	..
,, *prampramiana*	×	..	..	..	..	..	..	..	..	..	..
Spirorbis sp.	Augener (1918) from the Cape Coast Castle.										

4. SYSTEMATIC PART

(a) *Key to Families of Polychaeta*

The following key has been adapted from Fauvel (1923 and 1927*a*). It includes families not collected in the present survey and these have been marked with an asterisk.

1. Some parapodia bearing elytra, the rest with dorsal cirri . . . . APHRODITIDAE.
   Parapodia without elytra . . . . *2.*

2. A fan-shaped group of broad, flattened chaetae (paleae) on all segments CHRYSOPETALIDAE.
   No such groups of chaetae . . . . *3.*
3. Prostomium not distinct; when present pedal cirri globular . . . . . *4.*
   Prostomium distinct . . . . *6.*
4. Parapodia biramous and achaetous; prostomium fused with the two succeeding segments and bearing 2 or 4 tentacular cirri containing aciculæ; pedalcirri absent. Pelagic . . . . TOMOPTERIDAE.*
   Parapodia uniramous, with chaetae and with globular cirri . . . . . *5.*
5. Pharynx armed . . . . PISIONIDAE.*
   Pharynx unarmed . . . . SPHAERODORIDAE.*
6. Body not normally divided into distinct regions; all segments alike except those near the mouth and the pygidium. Pharynx protrusible and normally armed with jaws. This group includes those families of the Polychaeta Errantia of Fauvel (1923) not given above . . . . *7.*

Body often divided into distinct regions and adapted to either a tubicolous or burrowing life, the head is, therefore, either greatly modified, with a wreath of tentacles or gills surrounding the mouth, or almost completely divested of cephalic appendages. Parapodia much modified in the tubicolous forms in which the neuropodia are often in the form of pinnules (tori) bearing hooks or uncini. Without jaws. This group includes the Polychaeta Sedentaria of Fauvel, 1927*a* . . . *15.*

7. Prostomium conical, without antennae or palps ; dorsal and ventral cirri foliaceous ; chaetae rare, when present simple, acicular. Pelagic . . TYPHLOSCOLECIDAE.*

Prostomium with tentacles, usually with palps . . . *8.*

8. Prostomium small with three antennae ; pharynx unarmed ; a caruncle almost always present. Chaetae simple, calcareous in some genera . AMPHINOMIDAE.

Prostomium prominent ; without a caruncle . . . *9.*

9. Prostomium long, conical, annulated, with four short terminal antennae GLYCERIDAE.

Prostomium not so . . . *10.*

10. Proboscis without chitinous teeth . . . *11.*

Proboscis with chitinous teeth . . . *14.*

11. Parapodia normally uniramous, cirri usually foliaceous . . . *12.*

Parapodia biramous or very much reduced . . . *13.*

12. Prostomium with two very large globular eyes. Pelagic . . . ALCIOPIDAE.*

Prostomium with two small eyes . . . PHYLLODOCIDAE.

13. Parapodia biramous, with inter-ramal cirri (branchiae) . . . NEPHTHYDIDAE.

Parapodia biramous, or very much reduced, without branchiae . . HESIONIDAE.

14. Proboscis with one pair of heavy curved jaws distally and normally with paragnaths on its dorsal and ventral surfaces . . . NEREIDAE.

Proboscis with a complex armature—a pair of ventral pieces and two, or frequently more, dorsal pieces . . . EUNICIDAE.

Proboscis with one large tooth, or crown of teeth, or both . . . SYLLIDAE.

15. Body clearly divided into distinct regions . . . *23.*

Body not clearly divided into distinct regions . . . *16.*

16. Body very much swollen, few segments, filiform anal branchiae. A large ventral shield bordered with chaetae . . . STERNASPIDAE.

Body not swollen, numerous segments, without anal branchiae. No ventral shield . . . *17.*

17. Palps elongate . . . *18.*

Without palps . . . *22.*

18. Elongate palps (tentacular cirri) on the body, not on the prostomium . CIRRATULIDAE.

Elongate palps on the prostomium . . . *19.*

19. A cephalic cage formed by the chaetae of the first chaetigers . FLABELLIGERIDAE.

Without a cephalic cage . . . *20.*

20. Without branchiae. Prostomium oval, spoon shaped. Palps with sucker-like papillae . . . MAGELONIDAE.*

With branchiae . . . *21.*

21. Parapodial lamellae erect, dorsal. Branchiae cirriform. Hooded hooks and capillary chaetae . . . SPIONIDAE.

Anterior parapodial lamellae frilled or flask-shaped. Branchiae filliform. Chaetae of many kinds, plumed, spiny, barbed and acicular, etc. . . . DISOMIDAE.*

22. One median antenna. Dorsal foliaceous branchiae. Hooded hooks and capillary chaetae . . . PARAONIDAE.*

Two antennae or none. Capillary and forked chaetae, no hooded hooks SCALIBREGMIDAE.*

Prostomium blunt, without appendages or with a crown of lobes. No branchiae. Ventral tori with rows of uncini. Sandy tube . . . OWENIIDAE.

Prostomium without appendages, with a keel or rimmed cephalic plate . MALDANIDAE.

23.	A terminal branchial tuft with numerous filaments. Thoracic uncini dorsal; abdominal uncini ventral	32.
	No terminal branchial tuft	24.
24.	Paleae forming an operculum to close the tube	31.
	No opercular paleae	25.
25.	Prostomium without processes. Branchiae on many segments, but not on the prostomium	26.
	Prostomium with processes, either branchiae or tentacular filaments	29.
26.	With uncini	28.
	Without uncini	27.
27.	With acicular hooks or capillary chaetae	ORBINIIDAE.
	With no acicular hooks, only capillary chaetae	OPHELIIDAE.
28.	Prostomium blunt. Non-retractile arborescent branchiae in the middle body region	ARENICOLIDAE.*
	Prostomium conical. Branchiae, if present, posterior in position, simple or multifid, if multifid retractile	CAPITELLIDAE.*
29.	Body divided into 2–3 strikingly dissimilar regions. Prostomium with or without 2 small tentacles. Two long grooved palps. Anterior region short with uniramous feet bearing peculiar chaetae in the 4th chaetiger. Posterior notopodia erect. Uncini comb-like	CHAETOPTERIDAE.*
	Body divided into regions which are not strikingly dissimilar. With numerous tentacular filaments	30.
30.	Tentacular cirri retractile into the mouth. Prostomium distinct	AMPHARETIDAE.
	Tentacular cirri not retractile into the mouth. Prostomium indistinct	TEREBELLIDAE.
31.	An operculum of one anterior row of golden paleae	AMPHICTENIDAE.
	An operculum of two stalks bearing a crown of paleae	SABELLARIIDAE.
32.	Tube calcareous, normally with an operculum	SERPULIDAE.
	Tube membranaceous or mucous, never with an operculum	SABELLIDAE.

(b) *Glossary of Terms*

The following glossary includes only those terms which are not normally to be found in a standard text-book of zoology or English Dictionary.

ACICULA: A stout chaeta of one piece, almost always tapering to a blunt point.

CAPILLARY CHAETA: Simple chaeta, normally long and slender.

CARUNCLE: A longitudinal ridge on the dorsal surface of the prostomium and sometimes extending to some of the following segments.

CHAETA: A bristle made largely of chitin but exceptionally some may be composed of calcium carbonate (e.g. *Eurythoe complanata*). Chaetae are either simple (of one piece), or compound (having two or more articulating pieces).

FALCIGER: The terminal article of a compound chaeta when it is short and broad. *c.f.* SPINIGER.

HETEROGOMPH: The condition when the two lateral branches of the articulating surface of the main stem of a compound chaeta are unequal in length.

HOMOGOMPH: The condition when the two lateral branches of the articulating surface of the main stem of a compound chaeta are equal in length.

LIMBATE: The condition when a simple chaeta is bordered along all or part of its length, e.g. *Apomatus similis*, Text-fig. 30, *f*.

PALEA: A stout simple chaeta, groups of which appear in the Chrysopetalidae, Amphictenidae, Ampharetidae and Sabellariidae.

SESQUIRAMOUS: Condition of a parapodium when the dorsal component (notopodium) is reduced to a few chaetae or an acicula.

SPINIGER: The terminal article of a compound chaeta when it is long and slender. *c.f.* FALCIGER.

STYLODE: A dorsal appendage of the branchial filaments in some Sabellidae.

UNCINUS: A short simple chaeta which may be sigmoid, with teeth at the tip, or plate-like with rows of teeth along one edge.

(c) *Descriptions of Species*

Keys to genera and species have been compiled only in respect of forms actually recorded from the Gold Coast, or where systematic considerations suggest that details of related forms will be of help to the student.

Examples of all species have been deposited in the collections of the B.M. (N.H.), Reg. Nos., 1953.3.1.1–1234; duplicate material covering the majority of species, has been deposited in the Zoology Dept., University College, Achimota, Gold Coast.

Family APHRODITIDAE

Prostomium normally with four sessile, or pedunculate, eyes, one to three antennae and two palps inserted ventrally. Protrusible proboscis crowned with papillae and with four chitinous jaws (except the Aphroditinae). A feature of this family is the possession of elytra on the dorsal surface of the parapodia. The first pairs are always attached to segments 2, 4, 5 and 7, thereafter the arrangement varies, posteriorly they may be absent. Parapodia biramous, exceptionally reduced.

KEY TO SUBFAMILIES

1. Body short, fat and oval, jaws absent or rudimentary. Elytra may be covered with a thick mat of felt . . . . APHRODITINAE.
   Body comparatively long and thin, pharynx with jaws. Elytra never covered with a mat of felt . . . . 2.
2. Compound chaetae in the neuropodia. Elytra on all segments posteriorly SIGALIONINAE.
   All chaetae simple. Elytra on every second or third segment, or entirely absent, from the posterior part of the body . . . . 3.
3. Elytra on every second segment in the posterior part of the body. Prostomial eyes sessile or stalked. Tubicolous in habit . . . . . . POLYODONTINAE.
   Elytra on every third segment in the posterior part of the body, or entirely absent. Prostomial eyes sessile, never stalked. Errantiate in habit . . POLYNOINAE.

Subfamily APHRODITINAE

One unpaired antenna, no laterals; a facial tubercle beneath the antenna. Elytra 15 pairs, rarely 20, inserted on segments 2, 4, 5, 7, 9–21, 23, 25, 28, 31, alternating with dorsal cirri.

KEY TO GENERA

1. Dorsal surface covered with a thick felt; dorsal notopodial chaetae ending in blunt points or with fine hooks . . . . *Aphrodite.*
2. No covering of felt; notopodial chaetae harpoon-shaped on elytrigerous segments *Hermione.*

Genus *APHRODITE* Linnaeus, 1758

Fifteen pairs of elytra. Eyes sessile or absent.

Aphrodite alta Kinberg, 1856

Aphrodite alta, McIntosh, 1924, pp. 5–6, from Cape of Good Hope waters.
Aphrodite alta, Monro, 1930, pp. 36–38, fig. 5*a–i*, from 64° 20′ 00″ S., 63° 01′ 00″ W.

LOCALITIES. Off Accra: Stn. 47 (1); Stn. 110 (1); Stn. 133 (1); all complete, 20 mm. long by 10 mm. wide.

This species is characterized by the lack of eyes, the dorsal notopodial chaetae which taper to a fine hooked point, and which appear to lie in the dorsal felt rather than to project through it, the thick bearded ends of the neuropodial chaetae and the posterior neuropodial chaetae with long alternating teeth. These features clearly distinguish the species from *A. aculeata* which Fauvel (1950) reported from Rio de Oro.

DISTRIBUTION. This appears to be the first record of *A. alta* from the W. coast of Africa, north of the Cape. Kinberg (1856) reported it from Rio de Janeiro.

Genus *HERMIONE* Blainville, 1828

Four pedunculate eyes. Fifteen pairs of elytra.

Hermione hystrix (Savigny), 1818

Hermione hystrix, Fauvel, 1923, pp. 35–36, fig. 11.

LOCALITY. Off Accra, Stn. 126 (12), all complete, measuring between 20–30 mm. long by 10–15 mm. wide.

There are two pairs of eyes, each pair carried on a peduncle, situated ventral to the antenna. Two types of notopodial chaetae are present on elytrigerous segments; one set, stout, curved and ending in a simple point, the others with strong, harpoon-shaped points. On cirrigerous segments there are only thin chaetae with simple points. Neuropodial chaetae are bifurcate with a short limb and a long curved one which may be toothed on anterior and posterior feet.

DISTRIBUTION. Mediterranean Sea, Atlantic Ocean and Indo-Pacific regions.

Subfamily POLYODONTINAE

Bilobed prostomium, with four sessile eyes, or two large ommatophores and three antennae. Elytra on segments, 2, 4, 5, 7, 9, etc.

Only one genus of this subfamily has been recorded from the Gold Coast, *Panthalis*, but the following Key is included here to illustrate the difference between it and *Polyodontes*.

1. Superior neuropodial chaetae elongate hastate, the tip smooth or more or less hirsute *Polyodontes*.
2. Superior neuropodial chaetae penicillate (Text-fig. 1) . . . . . . *Panthalis*.

Hartman (1939) has drawn attention to the need for revising the diagnostic generic characters in this subfamily and this Key has been adopted from her suggestions. Thus the presence or absence of branchial lobes is of doubtful value, for many specimens are incomplete when collected and the methods adopted for preservation frequently result in the complete retraction of these organs.

Genus ***PANTHALIS*** Kinberg, 1855

Panthalis bicolor Grube, 1877

Polyodontes bicolor, Augener, 1918, pp. 119–125, pl. 2, fig. 28 ; pl. 3, fig. 47 ; text-fig. 4. From Accra.

Localities. Off Accra, Stn. 33 (1), anterior fragment 23 mm. in length ; Buchanan Survey, in a depth of 3·6 to 11·0 metres (1), anterior fragment, 10 mm. long ; Buchanan Survey, in a depth of 10 metres off lighthouse (1), anterior fragment, 17 mm. long.

The prostomium carries two large anterior ommatophores (eye-stalks) and two small posterior eye-spots, situated on either side of the median antenna, which projects forward between the ommatophores. Two lateral antennae are ventral to the eye-stalks. There are two pairs of tentacular cirri. Spinning glands are present in the feet. Neuropodial chaetae are illustrated in Text-fig. 1, (*a*) superior penicillate with the tip frequently carried beyond the bushy portion, (*b*) median stout aristate, (*c*) inferior serrulate.

No tubes were found with these specimens.

Distribution. The species is known only from the tropical West African coast.

Subfamily Sigalioninae

Elytra numerous, attached to segments 2, 4, 5, 7, etc., and on each segment from the 23rd–29th up to the end of the body. All the genera here reported have three antennae ; other genera, however, have one (*Pholoë*) or two (*Sigalion*).

Key to Genera

1. With a dominated cirrus on the 3rd chaetiger . . . . *2.*
   Without a dorsal cirrus on the 3rd chaetiger . . . . *3.*
2. With the unpaired antenna inserted on the anterior margin of the prostomium *Euthalenessa.*
   With the unpaired antenna inserted on the middle of the prostomium, in line with, or posterior to, the eyes . . . . *Eusigalion.*
3. With falcigerous compound chaetae in the neuropodium . . . . . *Sthenelais.*
   With spinigerous compound chaetae in the neuropodium . . . . . *Leanira.*

Genus ***EUTHALENESSA*** Darboux, 1899

The median unpaired antenna, without ceratophore or ctenidia, is on the anterior margin of the prostomium. From the fourth chaetiger dorsal ctenidia are present on the parapodia ; on the third foot there is a branchial tubercle but no true dorsal cirrus.

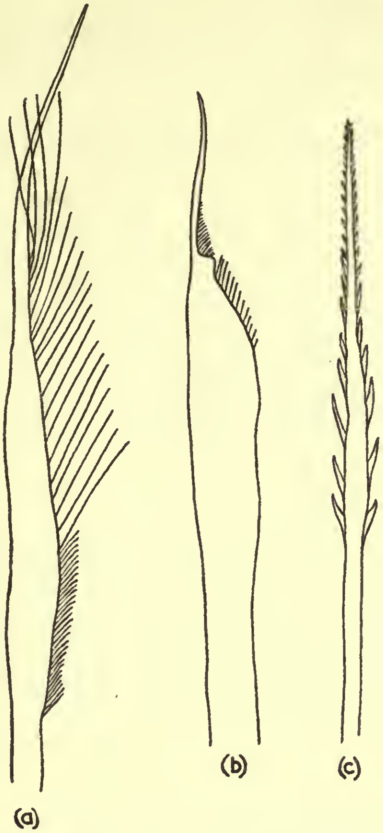

FIG. 1. *Panthalis bicolor.* Neuropodial chaetae; (*a*) superior penicillate; (*b*) median aristate; (*c*) inferior serrulate, × 200. (Specimen from the Buchanan Survey.)

Euthalenessa insignis Ehlers, 1908

Euthalenessa insignis Augener, 1918, pp. 108–112, from Apam.

This species has not been found in the present collections.

The specimens described by Augener were characterized by the possession of a third cirrus on the first chaetiger, and it is doubtful if this character is applicable to Ehler's species, but specimens will have to be examined before the true identity of Augener's record can be established.

Genus ***EUSIGALION,*** Augener, 1918

The median antenna is in the middle of the prostomium, between, or posterior to, the eyes. This character is here taken to separate *Eusigalion* from *Euthalanessa,* which are similar in other respects.

Eusigalion vazensis Augener, 1918

Eusigalion vazensis Augener, 1918, pp. 113–118, pl. 2, fig. 14; pl. 3, figs. 44–46; text-fig. 3. From Fernand Vaz in the French Congo.

LOCALITY. Off Accra, Buchanan survey, in 3·6 to 11·0 metres depth (2), anterior pieces, 20–23 mm. long.

There are about 12 pinnate filaments on the outside edge of each elytron. Antennae are very short, the unpaired median is set back on the dorsal surface of the prostomium, between the two pairs of small eyes; the paired anterior antennae project from the front border of the prostomium. Notopodial simple chaetae are long, barred and serrated. Neuropodial chaetae are in two groups; a supra-acicula group of simple spinose bristles and long-shafted compound forms with numerous joints, and a sub-acicula group, all compound, one set with single long-shafted, bifid, terminal articles, the other with numerous articles of which the terminal one is also bifid.

DISTRIBUTION. Only known from the above records.

Genus *STHENELAIS* Kinberg, 1855

Prostomium with four eyes. The lateral antennae are fused with the first chaetiger. Unpaired median antenna with basal ctenidia. Two long palps with ctenidia at the base. Branchiae on all parapodia from the fourth. Notopodial chaetae simple; neuropodial chaetae compound falcigers with sometimes a superior group of simple bristles.

KEY TO SPECIES

1. Elytra with simple fringes and entire borders . . . . *S. boa.*
2. Anterior elytra with bifid fringes; elytra from the 24th chaetiger with outside border notched . . . . *S. limicola.*

Sthenelais boa (Johnston), 1833

Sthenelais boa, Fauvel, 1923, pp. 110–111, fig. 41, *a–l*.

LOCALITY. Tenpobo shore, 6.ii.50 (1), 43 mm. long.

Elytra normally reniform, crossing and overlapping on the back, with minute papillae and with simple fringes on the outer border. Notopodial chaetae simple, finely spinous. Superior neuropodial chaetae simple, bi-pectinate, strongly spinous, the middle group compound falcigers with single bidentate articles, the inferior group also compound with long, pseudo-multiarticulate, bidentate falcigers.

Distribution. English Channel, Mediterranean Sea, Atlantic Ocean, Indian Ocean.

Sthenelais limicola (Ehlers), 1864

Sthenelais limicola, Fauvel, 1923, pp. 113–114, fig. 42, *a–g*.

LOCALITY. Off Accra, Buchanan Survey, in 3·6–11·0 metres depth (4), two complete, 60, 75 mm. in length, two fragments 23 and 56 mm. long.

The characters noted in the above key serve to separate this species from *S. boa*; in other characters the species are similar.

DISTRIBUTION. North Sea, Mediterranean Sea, Atlantic Ocean.

Genus *LEANIRA* Kinberg, 1855

Members of this genus may, or may not, have eyes; otherwise they are similar to *Sthenelais*, except as keyed above.

KEY TO SPECIES

1. Superior neuropodial chaetae simple, with whorls of spikes; inferior neuropodial chaetae compound, caniculate spinigers . . . . *L. japonica.*
2. All neuropodial chaetae compound, caniculate spinigers . . . . *L. yhleni.*

Leanira japonica McIntosh, 1885

Sthenolepis japonica, Willey, 1905, pp. 259–260, pl. 2, fig. 49.
Leanira japonica, Fauvel, 1932, pp. 33–34.

LOCALITIES. Off Accra, Stn. 57 (1); Stn. 70 (3); Stn. 97 (1); Stn. 132 (1); Stn. 133 (2). One of the specimens from Stn. 70 is complete, 64 mm. in length. All others are fragmentary, up to 15 mm. long.

Prostomium with four eyes. The dorsal cirrus is replaced in this species by a very small tubercle. The elytra, which are fringed, overlap but do not cross, and leave a considerable area of the mid-dorsal surface exposed. Notopodial chaetae are long and slender, neuropodial compound chaetae have long caniculate terminal pieces and a superior group of simple chaetae, with whorls of spikes, on most parapodia.

DISTRIBUTION. Previously reported from Japan, Malaya, Bay of Bengal and the Arabian Sea, this appears to be the first record of this species from the Atlantic Ocean.

Leanira yhleni Malmgren, 1867

Leanira yhleni, Fauvel, 1923, pp. 117–118 (no figures).

LOCALITY. Off Accra, Buchanan Survey, 41·4 metres depth, off Lagoon, (1), anterior fragment 25 mm. long.

This species is distinguishable from *L. japonica* as noted above in the key, and in having the anterior pair of eyes larger than the posterior pair. In *L. japonica* the posterior eyes are larger than the anterior. In both species the anterior eyes are near the front border of the prostomium, partly hidden beneath the antennal ctenidia, and the posterior pair are at the base of the unpaired antenna.

DISTRIBUTION. Bay of Biscay, Mediterranean Sea, Adriatic Sea; this appears to be the first record from the equatorial Atlantic.

Subfamily POLYNOINAE

Elytra 12 or more pairs inserted on segments 2, 4, 5, 7, 9, to 23–26, thence on every third segment to the posterior end of the body. All genera here reported have one unpaired, median antenna and two paired, lateral antennae.

Key to Genera

1. Lateral antennae inserted ventrally; 15 pairs of elytra . . . . . . 2.
   Lateral antennae inserted terminally, continuous with the prostomial peaks . . 3.
2. Chaetae transparent as crystal, with spinous pouches . . . . *Scalisetosus.*
   Chaetae not transparent, without spinous pouches . . . . . *Harmothoë.*
3. Elytra numerous, more than 15 pairs, a large dorsal tubercle in the form of a T on the cirrigerous segments . . . . *Acholoë.*
   Elytra 12 pairs . . . . 4.
4. Segment 3 fused with the segments 2 and 4 dorsally . . . . . *Pareulepis.*
   Segment 3 not fused dorsally . . . . *Lepidonotus.*

Genus *SCALISETOSUS* McIntosh, 1885

The 15 pairs of elytra are inserted on segments 2, 4, 5, 7–23, 26–29–32, not covering the whole body. Neuropodial chaetae with semilunar cusps are slightly bifid at the extremity. Notopodial chaetae curved with blunt spines.

Scalisetosus pellucidus (Ehlers), 1864

Scalisetosus pellucidus, Fauvel, 1923, p. 74, fig. 27, *a–f*.

Locality. Off Accra, stn. 47 (1), 10 mm. in length.

Irregular dark brown transverse bands decorate the dorsal surface. Antennae and cirri are papillated. The ventral chaetae are not as deeply incised at their distal ends and the notopodial chaetae not so clearly notched as normal representatives of the species.

Distribution. Mediterranean Sea, Atlantic Ocean, Bay of Bengal, Malay Archipelago.

Genus *ACHOLOË* Claparède, 1870

Two pairs of tentacular cirri with basal aciculae. Elytra on segments 2, 4, 5, 7–23, 26, 29, 32, thence almost up to the end of the body. Parapodia with reduced notopodia.

Acholoë astericola (Delle Chiaje), 1823

Acholoë astericola, Fauvel, 1923, pp. 94–95, fig. 36, *d–h*.

Localities. Off Accra: From starfish, at 25 metres, and 10 metres (off Petrol Buoy), numerous specimens; Stn. 57 (1), among tubes of *Diopatra neapolitana;* Stn. 67 (1); Stn. 80 (1); Stn. 89 (1); Stn. 104 (1); Stn. 123 (1).

Most of these specimens are fragmentary, the complete ones measure up to 30 mm. long.

There are about 45 pairs of elytra. Neuropodial chaetae have a recurved unidentate tip with a short spinous region, and notopodial chaetae are short with transverse rows of pinnules.

Distribution. English Channel, Mediterranean Sea, Atlantic Ocean.

Genus *PAREULEPIS* Darboux, 1899

Segment 3 fused with segments 2 and 4 dorsally. Elytra on segments 2, 4, 5, 7, 9, 11–21–24. Notopodial chaetae are slender capillaries and stout curved bristles bent abruptly at their distal ends. Neuropodial aciculae are short, wholly embedded, with extended, plate-like terminations. Neuropodial chaetae include a few small, laterally pectinate, bristles, and a bundle of almost straight chaetae.

Pareulepis geayi (Fauvel), 1918

Eulepis geayi, Fauvel, 1919, pp. 335–339, pl. 15, figs. 17–21 ; pl. 17, figs. 76–79.

LOCALITY. Off Accra, Buchanan Survey, between 11–13 metres depth, off Christiansborg Castle (2), each about 25 mm. long.

The arrangement of anterior segments in this species is shown in Text-fig. 2. Thus segment 3 is represented laterally by parapodia, but is fused dorsally with segments 2 and 4. Elytra are present therefore on segments 2, 4, 5, 7, 9–21–24, after which there are ten cirrigerous segments up to the end of the body. The elytra on segment 24 extends from segment 23 backwards to 29, so that only a small posterior portion of the worm remains uncovered. There are up to 12 marginal papillae on the outside border of each elytron. Dorsal cirri are stout and foliaceous throughout.

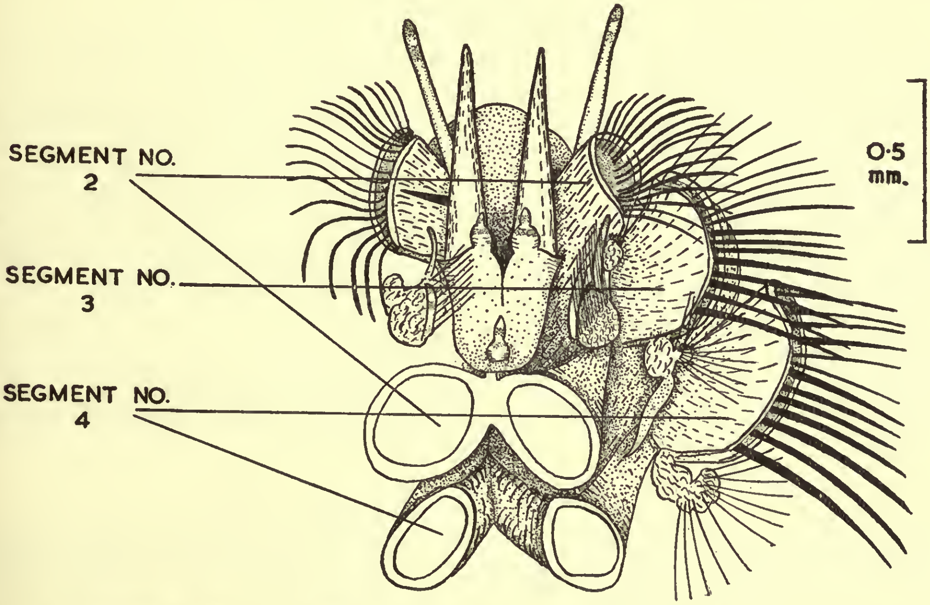

FIG. 2. *Pareulepis geayi*. Dorsal view of anterior segments to show the fusion of segment 3 with segments 2 and 4 dorsally. Elytra and the 2nd and 3rd parapodia on the left-hand side have been omitted.

The specimens here described have been referred to this species, and not to *P. fimbriata* Treadwell, with which Hartman (1939) considers *P. geayi* synonymous, because of the position of the unpaired median antenna. Fauvel (1919, p. 338) clearly implies that the unpaired antenna is posterior to the median line of the prostomium. Treadwell (1900, p. 190), however, places it on the anterior prostomial margin. Too, Treadwell's specimens had eye-spots; these are not present in Fauvel's species.

DISTRIBUTION. This species appears to have been recorded only from the Indo-Pacific region, though the genus, through *P. fimbriata*, is also known from the Pacific coast of America.

Genus ***LEPIDONOTUS*** Leach, 1816

Prostomium bilobed, without frontal horns, four eyes. Twelve pairs of elytra attached to segments 2, 4, 5, 7–21, 23.

Lepidonotus hupferi Augener, 1918

Lepidonotus hupferi Augener, 1918, pp. 133–136, pl. 2, figs. 7–11; text-fig. 5.

LOCALITIES. (1) Tenpobo shore (10), most complete, between 8–18 mm. in length, collected in February, 1950. (2) Off Accra, from wood netted off Chorkor in 14 metres, 14.v.51 (1), 10 mm. long. (3) Axim, (*a*) Shore, 13/14.iv.49 (1), 12 mm. long; (*b*) Hospital Reef (4), 2 complete, 4 and 6 mm. long; 2 parts 4 and 8 mm. long.

The elytra completely cover the dorsal surface, are fringed on their external margins, and covered with very small tubercles, with a broad base and slender stalk. Notopodial chaetae are slender and serrated. Neuropodial chaetae are stout with a serrulated blade; some are distally entire, others have a slightly bifid tip.

Fauvel (1950) has noted that this species appears to replace *L. squamatus* in the tropical zone.

DISTRIBUTION. Tropical West Africa, Western Mexico, Panama, N.W. South America. Hartman (1939) records this Western Hemisphere distribution from the intertidal zone to 22 metres.

Genus ***HARMOTHOË*** Kinberg, 1855

Prostomium bilobed, with four eyes, often with lateral peaks. Elytra covering all the dorsal surface on segments 2, 4, 5, 7–23, 26, 29, 32.

Harmothoë goreensis Augener, 1918

Harmothoë goreensis Augener, 1918, pp. 142–146, pl. 2, figs. 4–6; pl. 3, fig. 42; text-fig. 7.

LOCALITIES. Off Accra: (*a*) Stn. 47, (1), 8 mm. long; (*b*) from wood netted off Chorkor in 14 m., (4); (*c*) 2 miles out from R. Densu, 8.iv.49, 14·6 m., in shingle, (4), 2 complete, 6 mm. long; (*d*) 2 miles west out from R. Densu, 1 mile off shore, 2.iii.49, 7·3 m., (1), 4 mm. long.

The elytra have short fringes on their external margins; elytron tubercles are sac-like in shape with a minute distal pore. Tentacular cirri, dorsal cirri and palps are covered with papillae. Neuropodial chaetae are normally bidentate superiorly and inferiorly are unindentate. Notopodial chaetae (always stouter than neuropodial bristles in *Harmothoë*) are distally entire and heavily serrated.

DISTRIBUTION. Previously recorded from Senegal and Angola.

Family CHRYSOPETALIDAE

Dorsal surface of the segments bearing a fan or transverse row of paleae. Prostomium with four eyes and three antennae. Biramous parapodia, with dorsal cirri on all segments.

Genus **BHAWANIA** Schmarda, 1861

The head is exceedingly small and not easily seen ; the elongated body consists of numerous segments. Neuropodial chaetae are compound.

Bhawania goodei Webster, 1884

Bhawania goodei, Augener, 1918, pp. 98–103, pl. 2, figs. 1–2 ; text-fig. 1 ; from Pram Pram.

LOCALITIES. (1) Accra, Christiansborg shore (1), almost complete, 8 mm. long. (2) Axim, Hospital Reef, 7.i.51 (1), middle body piece, about 14 mm. long.

It has not been possible to examine the head in either of these specimens, since, in the specimen from Accra, it has been damaged and it is missing from the Axim example. The neuropodial heterogomph spinigers and falcigers are as figured by Augener, but the paleae, which are of one type, are as shown in Text-fig. 3 and not as illustrated by Augener. Monro (1933) noted that the tips of the paleae were not emarginate.

DISTRIBUTION. Apart from the above records *B. goodei* has been recorded from Bermuda and False Bay, South Africa, in the Atlantic Ocean, and from the Galapagos Islands and Taboga Island, Panama Bay, in the Pacific Ocean.

Family AMPHINOMIDAE

Body depressed, prostomium deeply set into the anterior segments, carrying three antennae, two palpal pads and a caruncle. Biramous parapodia with branchiae and simple chaetae (exceptionally uniramous with compound hooks).

KEY TO GENERA

1. Body short and oval ; branchiae pinnate . . . . *Chloeia.*
   Body long and vermiform ; branchiae bushy . . . . 2.
2. Branchiae beginning on the 1st chaetiger ; caruncle cushion-like, with dorsal surface with chevron crenulations . . . . *Hermodice.*
   Branchiae beginning on the 2nd. or 3rd. chaetiger ; caruncle with a ventral crenulate portion . . . . *Eurythöe.*

Genus **CHLOEIA** Savigny, 1818

Caruncle a plaited crest on a horizontal plate.

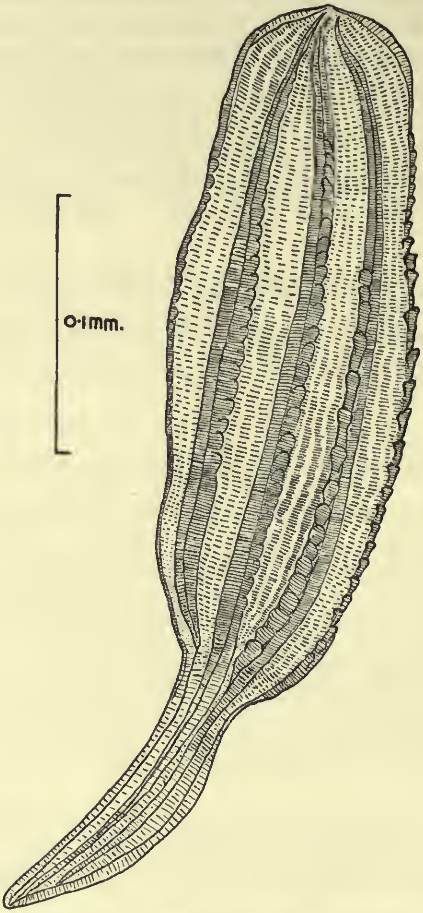

FIG. 3. *Bhawania goodei*. One of the paleae from the dorsal surface. (Specimen from Axim.)

Chloeia viridis Schmarda, 1861

Chloeia euglochis, Ehlers, 1887, pp. 18–24, pl. 1, figs. 1–2; pl. 2, figs. 1–8; pl. 3, figs. 1–4.
Chloeia euglochis, Augener, 1918, pp. 94–95, from Gorée, Senegal.

LOCALITY. Off Accra, Buchanan Survey, in 40 metres off Christiansborg (1), 70 mm. long by 10 mm. wide.

This is one of the few species of Polychaeta in which the pigment is retained, even after long periods in preservative fluid. Thus, in this single specimen, the dorsal cirri are violet, the pinnate gills, which appear at the fifth chaetiger, edged with purple, whilst the superior neuropodial chaetae are a brilliant orange, as are a few in the notopodial group. The remaining chaetae are glistening white, and the worm presents a striking appearance. The caruncle is attached to the body to the second chaetiger, though its unattached portion projects for 2–3 more segments, and it is surmounted throughout its length by a conspicuous, mid-dorsal, dark purple line. Another thin mid-dorsal purple line, which is slightly broken in the intersegmental furrows, extends along the back of the worm.

DISTRIBUTION. This species is also known from the W. Indies, Gulf of California, Galapagos and Cocos Islands.

Genus ***HERMODICE*** Kinberg, 1857

Caruncle cushion-like, with chevron crenulations on the dorsal surface.

Hermodice carunculata (Pallas) var. ***didymobranchiata*** (Baird), 1864

Amphinome didymobranchiata Baird, 1864, pp. 449–450, pl. 45, figs. 1–7; from Ascension Island.

Hermodice carunculata var. *didymobranchiata*, Fauvel, 1914, pp. 113–116, pl. 8, figs. 22–27, 31–32; from the Gulf of Guinea.

Hermodice carunculata var. *didymobranchiata*, Monro, 1930, p. 27; from the Gulf of Guinea and the French Congo.

LOCALITIES. Off Accra: Stn. 47 (3), 12, 20 and 30 mm. long; Stn. 115 (6), largest 40 mm. long, smallest 16 mm.; Stn. 131 (1), 25 mm. long; Stn. 133 (3), 2 complete, about 20 mm. long.

Most of these specimens have lost their colour except for the thin dark intersegmental bands on the back. The caruncle extends to the 4th chaetiger. Separation of the branchiae into two bushy lobes instead of one and the almost complete absence of harpoon-shaped dorsal chaetae, separates this variety from the stem species.

DISTRIBUTION. This variety appears to have been recorded only from the above listed areas.

Genus ***EURYTHOË*** Kinberg, 1857

Caruncle with vertical folds along the lateral walls, and with a vertical crenulate portion.

KEY TO SPECIES

1. Branchiae beginning on the second segment. Caruncle terminating on the third or fourth segment. Four eyes . . . . *E. complanata.*
2. Branchiae beginning on the third segment. Caruncle terminating on the first segment. Four eyes . . . . *E. parvecarunculata.*

Eurythoë complanata (Pallas), 1766

Eurythoë complanata, Augener, 1918, pp. 88–89; from the Islands of Rolas and Annobon.

Eurythoë complanata, Fauvel, 1932, pp. 45–46.

LOCALITIES. (1) Tenpobo shore (70 +). (2) Dixcove shore (7). (3) Axim, (*a*) Hospital Reef (1), posterior fragment; (*b*) Shore (1), small specimen.

These specimens vary considerably in length, the largest being about 100 mm. long, and the smallest 15 mm.

Notopodial chaetae are of three types: (*a*) stout, straight and blunt; (*b*) long and calcareous, with a slender tip having a slight spur at the base; (*c*) long harpoon-shaped, with lateral rows of teeth, and neuropodial chaetae of two forms: (*a*) stout furcate chaetae with unequal arms; (*b*) a few subfurcate with one arm thin and elongated.

DISTRIBUTION. This species is well known from littoral regions of the tropical Atlantic, Pacific and Indian Oceans.

Eurythoë parvecarunculata Horst, 1912

Eurythoë parvecarunculata, Augener 1918, pp. 90–93, pl. 2, fig. 3; pl. 3, figs. 37, 38, from Cameroons and Spanish Guinea.

Eurythoë parvecarunculata, Fauvel 1927*b*, pp. 525–526, fig. 1 *a–h*, from Cameroons and French Guinea.

LOCALITIES. Off Accra: Stn. 12 (1), anterior piece 17 mm. long; Stn. 16 (2), anterior pieces 10 mm. and 15 mm. long; Stn. 32 (3), two 20 mm. long, one 30 mm. long; Buchanan Survey, off Accra, in $3\frac{1}{2}$–11 metres, (1).

There are stout, harpoon-shaped, and slender, elongated, bifurcated chaetae in the notopodial group. The bifurcation in the slender bristles may be reduced to a spur. The neuropodial chaetae are furcate, slightly denticulate.

DISTRIBUTION. This species is also known from the Indian Ocean, from Natal to Malaya.

Family PHYLLODOCIDAE

Body normally long and slender with numerous segments. Prostomium variable in outline, with two eyes and four or five antennae. Smooth or papillate proboscis, protrusible and unarmed. Segments 1–3 bearing tentacular cirri. Parapodia uniramous, with foliaceous dorsal cirri and compound chaetae.

KEY TO GENERA

1.	With 4 pairs of tentacular cirri	2.
	With 2 pairs of tentacular cirri	*Eteone*.
2.	With 5 antennae	*Eulalia*.[1]
	With 4 antennae	*Phyllodoce*.

[1] Not recorded from the Gold Coast.

Genus ***PHYLLODOCE*** Savigny, 1822

The four pairs of tentacular cirri are arranged on the three segments—1 : 2 : 1. Two anal cirri.

KEY TO SUBGENERA

1.	Protruded proboscis proximally set with longitudinal rows of papillae	(*Anaitides*).
2.	Protruded proboscis proximally set with diffuse papillae	(*Phyllodoce*).

KEY TO SPECIES OF *Anaitides*

1.	With more than 12 rows of papillae forming a continuous series around the proximal half of the proboscis	*A. africana*.
2.	With 12 rows of papillae arranged in two lateral groups of 6 on the proximal half of the proboscis	*A. oculata*.

Phyllodoce (Anaitides) africana Augener, 1918

Phyllodoce africana Augener, 1918, pp. 171–174, pl. 2, fig. 25; pl. 3, fig. 49–51; text-fig. 11.

LOCALITY. Off Accra, Stn. 52, (1), incomplete, 24 mm. long.

The protruded proboscis is provided with a crown of six large bulbous papillae, from which run six longitudinal rows of eight similar papillae. These rows are followed by 24 longitudinal rows of about 14 much smaller papillae. Dorsal cirri broadly foliaceous throughout, ventral cirri slender, those situated posteriorly acquiring a pointed tip.

DISTRIBUTION. This species has been previously recorded only from Angola and Senegal.

Phyllodoce (Anaitides) oculata Ehlers, 1887

Phyllodoce (*Anaitides*) *oculata*, Augener, 1918, pp. 169–171, pl. 3, figs. 57–58, from Accra.

This species has not been found in the present survey.

Distally the proboscis is similar to the condition in *A. africana*, but the proximal portion has only 12 rows of papillae, and these are disposed in two lateral groups of six. Dorsal cirri become slender in the middle of the body.

DISTRIBUTION. The W. Indies, Gulf of Guinea, Ascension Island and Tristan da Cunha.

Genus ***ETEONE*** Savigny, 1822

Dorsal cirrus absent on the 2nd segment. Proboscis smooth, or with soft papillae and small cuticularized tubercles.

KEY TO SUBGENERA

1. Proboscis smooth or with soft papillae . . . . (*Eteone*).
2. Proboscis with lateral rows of large soft papillae and small spinous tubercles . (*Mysta*).

Eteone (Mysta) picta Quatrefages, 1865

Eteone (*Mysta*) *picta*, Fauvel, 1923, pp. 176–177, fig. 64, *a–g*.

LOCALITIES. Off Accra: Stn. 57 (1), 15 mm. long, incomplete; Stn. 69 (2), 1 complete 17 mm., the other incomplete, 37 mm. long; Buchanan Survey, 3·6 to 11·0 metres (4), 3 complete, 31, 38 and 42 mm. long.

For description these specimens may conveniently be divided into two groups: one representing the young or immature form, the other the adult or sexually mature condition.

(*a*) *The immature forms* (from Stns. 57 and 69). In these specimens the prostomium bears two clear indentations on either side. The protruded proboscis is crowned by an encircling group of large soft papillae, whilst two longitudinal rows of equally large papillae extend laterally along the greater part of its length. Elsewhere there are small papillae with soft chitinous teeth (Text-fig. 4, *a*). The dorsal surface of the body in the specimen from Stn. 69 is marked with pale red-brown lateral stripes, although the effect of preservation may give the uniform stripes a speckled appearance. In the specimen from Stn. 57 the colour is uniformly light brown, with dark markings towards the sides. All specimens have the base of the foliaceous dorsal cirrus coloured in pattern with the colouration of the adjacent dorsal surface of the body. The remainder of the dorsal cirrus is greyish white or yellow, there being a suture between these two clearly defined areas. Compound chaetae have long terminal articles and project much further from the body than the cirri. On the articulating surface of the main stem of the chaetae there are two teeth, as well as a small finely pectinate plate (Text-fig. 4, *b*).

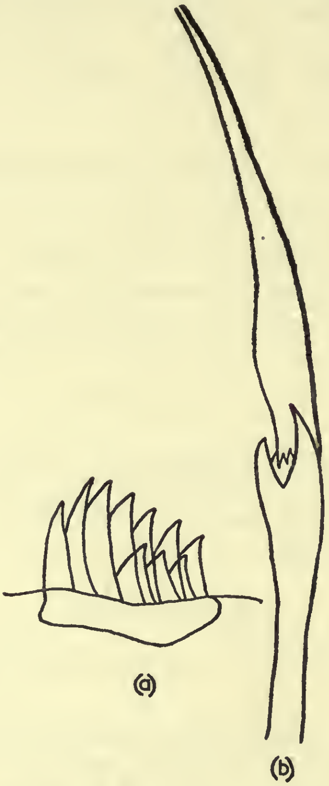

FIG. 4. *Mysta picta.* (*a*) Small papilla, with chitinous teeth, from the proboscis, × 700; (*b*) compound chaeta, × 500. (Specimen from Stn. 69.)

(*b*) *The sexually mature forms* (Buchanan Survey collections). In two of these specimens the colour pattern is similar to that in the specimens described in group (*a*), but the posterior parapodia contain small eggs, in which the nuclei are not visible. The suture on the dorsal cirrus, however, is clearly seen and appears to segregate a basal sac-like portion from a terminal solid piece. One of the remaining specimens has much longer dorsal cirri extending posteriorly from the middle of the body. In the anterior and middle regions of the dorsal surface the body is without colour but gradually becomes light bronze posteriorly. The lateral body-wall and the basal sac-like portion of the parapodia, from behind the middle region of the body are rich blood red, whilst the tips of the dorsal cirri are yellow. The basal portion contains numerous large eggs, with visible nuclei ; the eggs are so large and numerous that they produce a considerable swelling of the body-wall. The remaining specimen has very much enlarged dorsal cirri from the 37th chaetiger, at which point the dorsal body-wall and the bases of the parapodia have assumed a bronze colour, whilst the tips of the dorsal cirri are yellow. Anterior to the 37th chaetiger the colour is similar to that in specimens described in group (*a*). The parapodia, posteriorly from the 37th chaetiger, all contain eggs, the number to each segment increasing towards the hinder end of the body, whilst the chaetae only project as far as the dorsal cirri. Constant reference has been made to the prominent suture on the dorsal cirrus in all the specimens here described, and examination of the mature specimens indicates that the eggs collect in the basal sac-like portion of the parapodia, and it is here suggested that the suture may represent the line of rupture when the eggs are liberated through the body wall, into the sea, for external fertilization.

That these specimens represent a series from the immature to the sexually mature condition is a supposition which can only be confirmed through observation on the living animal. But the conclusion here reached—that all the specimens are of the same species—appears justifiable, particularly when the variation in related genera and families during their life histories is considered.

DISTRIBUTION. This appears to be the first record of the species from the Equatorial Atlantic. Previously, *E.* (*M.*) *picta* has been reported from the North Sea, the English Channel, the west coast of Scotland, the Bay of Biscay and the Mediterranean.

Family HESIONIDAE

Body short, cylindrical. Prostomium simple or bilobed, normally with four eyes, two or three antennae and two biarticulate palps. Protrusible proboscis with or without jaws. Parapodia biramous, or reduced with long dorsal cirri and both simple and compound chaetae.

Genus ***LEOCRATES*** Kinberg, 1865

Prostomium with four eyes, three antennae and two palps. There are eight pairs of tentacular cirri. Proboscis with chitinous jaws. Parapodia biramous, notopodial chaetae simple, neuropodial chaetae compound.

Leocrates claparedii (Costa), 1868

Tyrrhena claparedii, Claparède, 1868, pp. 228–231, pl. 18, fig. 3.
Leocrates claparedii, Fauvel, 1923, pp. 237–238, fig. 88, *i–n*.

LOCALITY. Axim, Hospital Reef, 13.iv.49 (1), complete, 18 mm. long.

In this species the upper jaw plates have only one tooth, which distinguishes it from *L. atlanticus*, with two teeth, reported by Fauvel (1950) from Dakar. The median antenna in *L. claparedii* is short and subulate ; the paired laterals slender and slightly longer than the palps. Notopodial chaetae appear at the 5th chaetiger and are simple and spinous: neuropodial chaetae have a bidentate sickle-shaped terminal piece. There are 17 segments bearing parapodia, the last pair being achaetous, retaining only the notopodial and neuropodial cirri as parapodial appendages, which, with the two urites, gives the appearance of there being six anal cirri.

Augener (1918) reported a new species, *L. greeffianus*, from the Isle of Rolas, by St. Thomas, without noting the form of the pharyngeal armature.

Distribution. Originally recorded from Naples; Day (1934 and 1951) has collected this species from the coast of Natal. It may have been found in the Indo-Pacific region and reported under various names, but lack of details of the jaw structure makes confirmation of this impossible.

Family SYLLIDAE

Body small and narrow. Prostomium with four eyes, two palps and three antennae. Normally two pairs of tentacular cirri on the first segment, which never has chaetae. Protrusible proboscis, divided into two regions: (1) anterior, the pharynx, chitinous, cylindrical, with or without teeth; (2) posterior, the proventriculus, barrel-shaped. Parapodia uniramous, normally with dorsal and ventral cirri. Chaetae rarely simple, normally compound with a heterogomph articulation.

Key to Subfamilies

1.	Without ventral cirri	AUTOLYTINAE.[1]
	With ventral cirri	2.
2.	Palps not fused	SYLLINAE.
	Palps fused	3.
3.	Palps fused at the bases only	EUSYLLINAE.
	Palps fused along their entire length	EXOGONINAE.

[1] Not recorded from the Gold Coast.

Subfamily SYLLINAE

Key to Genera

1.	A large tooth with a trepan	TRYPANOSYLLIS.
	A large tooth with no trepan	2.
2.	With the tooth on the anterior part of the pharynx	SYLLIS.
	With the tooth on the posterior part of the pharynx	OPISTHOSYLLIS.

Genus ***TRYPANOSYLLIS*** Claparède, 1864

The proboscis is crowned with a circle of chitinous teeth (the trepan), and there is also a large single anterior tooth.

Trypanosyllis prampramensis Augener, 1918

Trypanosyllis prampramensis Augener, 1918, pp. 276–278, pl. 4, figs. 91–92, text-fig. 26; from Pram Pram.

Trypanosyllis prampramensis, Day, 1953, p. 414, from Still Bay and Kommetje, S. Africa.

This species is only known from these records, and has not been found in the present survey. *T. prampramensis* appears to be very close to the European *T. coeliaca*, but is characterized by unidentate compound chaetae, the latter having bidentate chaetae. Augener's specimen was 6·5 mm. long by 0·7 mm. wide for 100 segments.

Genus *SYLLIS* Savigny, 1818

Prostomium with four eyes and often two anterior eye-spots. Pharynx crowned with soft papillae and with a prominent anterior tooth. Antennae and dorsal cirri are moniliform; ventral cirri are not articulated.

KEY TO SUBGENERA

1.	All chaetae simple	(*Haplosyllis*).[1]
	With compound chaetae and, sometimes, simple chaetae	2.
2.	Anterior chaetae compound, thereafter some large simple chaetae	(*Syllis*).
	All chaetae compound	3.
3.	Compound chaetae with short articles all alike or differing only slightly from each other	(*Typosyllis*).
	Compound chaetae with long and short articles	(*Ehlersia*).

[1] Not recorded from the Gold Coast.

Syllis (Syllis) gracilis Grube, 1840

Syllis gracilis, Fauvel, 1923, p. 259, fig. 96, *f–i*.

LOCALITY. Off Accra, dredge in 7·3 metres, 1 mile off shore, 2 miles west of Densu River (1), 8 mm. long.

The dorsal cirri have between 8 and 12 articles. In the middle of the body chaetae are simple (Text-fig. 5, *a*), but anteriorly and posteriorly there are compound falcigers. The specimens here examined are not as long as those recorded by Fauvel (1923); they may be immature.

DISTRIBUTION. Mediterranean Sea, Atlantic Ocean, Red Sea, Indian and Pacific Oceans.

Subgenus *TYPOSYLLIS* Langerhans, 1879

KEY TO SPECIES

1.	Dorsal cirri long with more than 20 articles	*T. variegata*.
2.	Dorsal cirri short with less than 20 articles	*T. hyalina*.

Syllis (Typosyllis) variegata Grube, 1860

Syllis (*Typosyllis*) *variegata*, Fauvel, 1923, p. 262, fig. 97, *h–n*.

LOCALITIES. Axim, (*a*) Shore, 13.iv.49 (1), 10 mm. long, incomplete; (*b*) Hospital Reef, 7.i.51 (1), 7 mm. long, complete.

In the specimen from Axim shore, the dorsal cirri are alternately long and short, with 30 to 40 and 20 to 25 articles respectively. The specimen from the Hospital Reef, however, has dorsal cirri all about the same size with 30 to 40 articles. In both specimens the pharynx is crowned with 10 to 11 soft papillae and has a prominent anterior tooth. In the specimen from the Hospital Reef compound chaetae have strongly bidentate, short, terminal articles, but in the specimen from the shore the bidentation is less pronounced.

DISTRIBUTION. English Channel, Mediterranean Sea, Atlantic Ocean, Indian Ocean, Red Sea and Pacific Ocean.

Syllis (Typosyllis) hyalina Grube, 1863

Syllis (*Typosyllis*) *hyalina*, Augener, 1918, pp. 242–247, pl. 4, figs. 95, 96, from Pram Pram.

This species has not been collected in the present survey. It is distinguished from *T. variegata* in having unidentate terminal articles on the compound chaetea, and few articles on the dorsal cirri. *T. hyalina* frequently retains its colour after preservation, showing a uniform light red anteriorly, or transverse bands of a red-brown, but no specimens of *T. variegata* have been examined retaining any colouring matter.

DISTRIBUTION. English Channel, Mediterranean Sea and Atlantic Ocean.

Subgenus ***Ehlersia*** Langerhans, 1879

Syllis (Ehlersia) cornuta Rathke, 1843

Syllis (*Ehlersia*) *sexoculata*, Augener, 1918, pp. 269–271, from Pram Pram in 9 metres depth.

LOCALITIES. (1) Off Accra, dredge in 7·3 metres, 1 mile off shore, 2 miles west of Densu River, (1), 6 mm. long. (2) Axim shore, 13/14.iv.49, (2), 5 and 6 mm. long.

There are two pairs of small eyes posterior to the median antennae, and two minute eye-spots on the anterior border of the prostomium. Anterior dorsal cirri have 8 to 10 articles, median cirri 10 and posterior cirri 4 to 5. The two anal cirri have 12 articles. Compound chaetae are of two kinds, one with a long terminal article (Text-fig. 5, *b*) and the other short (Text-fig. 5, *c*).

These specimens are small and may be juveniles.

DISTRIBUTION. English Channel, Mediterranean Sea, Atlantic—Canaries, Senegal, Angola—Persian Gulf and Indian Ocean.

Genus ***OPISTHOSYLLIS*** Langerhans, 1879

An occipital flap on the posterior border of the prostomium.

Opisthosyllis brunnea Langerhans, 1879

Opisthosyllis brunnea, Augener, 1918, pp. 274–276, text-fig. 25.

LOCALITIES. (1) Tenpobo shore, 3/4.ii.50 (5), 3 complete, 8–10 mm. long. (2) Winneba shore, 22.xi.49 (1), complete, 13 mm. long. (3) Axim, Hospital Reef, 7.i.51 (1), incomplete, 6 mm. long.

There are between 30 to 50 articles in the dorsal cirri. The pharynx extends over eleven segments, bears a crown of 9 to 11 papillae and carries a large conical tooth

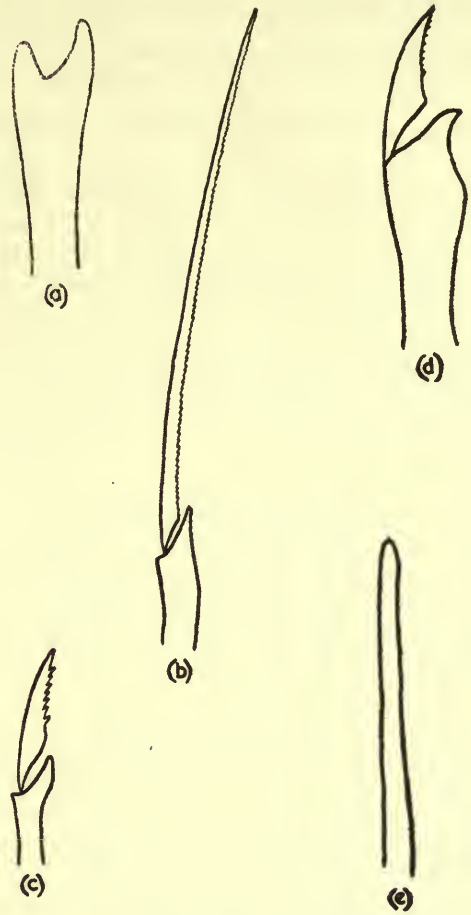

FIG. 5. Syllidae chaetae. (*a*) *Syllis gracilis*, simple chaeta, × 300. (*b*) *Ehlersia cornuta*, compound spiniger, × 400. (*c*) *Ehlersia cornuta*, compound falciger, × 400. (*d*) *Opisthosyllis brunnea*, compound falciger, × 250. (*e*) *Opisthosyllis brunnea*, simple chaetae, × 300.

posteriorly. The tooth is without colour and stands out against the dark brown of the pharynx. Compound chaetae have short unidentate articles (Text-fig. 5, *d*). In posterior parapodia there are long simple chaetae (Text-fig. 5, *e*).

DISTRIBUTION. The tropical coast of W. Africa and the Indian Ocean.

Subfamily EUSYLLINAE

Genus ***PIONOSYLLIS*** Malmgren, 1867

Pharynx with a single anterior tooth.

Pionosyllis ehlersiaeformis Augener, 1913

Pionosyllis ehlersiaeformis, Augener, 1918, pp. 281–283.
Pionosyllis ehlersiaeformis, Day, 1953, pp. 415–416, text-fig. 3, *d*.

LOCALITY. Off Accra, Buchanan Survey, in 14·5 metres off the Castle (1), incomplete, 15 mm. long.

The pharynx is crowned with eight large papillae. Antennae and dorsal cirri are very long with numerous articulations, which is unusual in this genus where, normally, the appendages are smooth. Ventral cirri are smooth and pointed. Superior chaetae have slender, curved unidentate terminal articles, about ten times as long as the articles on the inferior chaetae which are straight with bidentate tips.

No eyes have been seen in this specimen, otherwise it is typical of the species.

DISTRIBUTION. Augener originally recorded this species from S.W. Australia, but in 1918 he reported it from German S.W. Africa, and in 1953 Day collected it from Cape Agulhas.

Subfamily EXOGONINAE

Genus ***EXOGONE*** Oersted, 1845

Palps well developed, completely fused ; three antennae ; one pair of tentacular cirri. Pharynx with a single tooth. Dorsal and ventral cirri small. Chaetae simple and compound.

Exogone gemmifera (Pagenstecher)

Exogone gemmifera, Augener, 1918, pp. 299–301, text-fig. 29, from Pram Pram in 9 metres depth.

This species has not been collected in the present survey. Median antenna longer than the prostomium and longer than the paired laterals ; two pairs of large eyes. Dorsal cirri missing on the second chaetiger ; ventral cirri small, often difficult to see. Pharynx straight, crowned with papillae, with a single anterior tooth. In each parapodium there is a simple, bluntly terminated chaeta and a compound form with a very small bidentate article ; on posterior feet there is a simple ventral chaeta. *E. gemmifera* normally measures between 2–4 mm. in length.

DISTRIBUTION. English Channel, Mediterranean Sea, and Atlantic Ocean.

Family NEREIDAE

Prostomium with four eyes, two antennae, two massive palps and four pairs of tentacular cirri. Proboscis armed with two horny jaws and normally a series of horny teeth (paragnaths). Parapodia normally biramous after the 2nd foot ; chaetae compound ; most species have a Heteronereis, sexually mature form.

Generic and specific distinctions in this family are based primarily on the form and arrangement of the paragnaths. These are divided first into two rings, the maxillary and oral (Text-fig. 6), and then into eight numbered areas, of which I to IV are maxillary and V to VIII oral; odd numbers are median and single, even numbers lateral and paired. The jaws are at the distal end of the proboscis. The different types of chaetae referred to in the text are illustrated in Text-figs. 8 and 12.

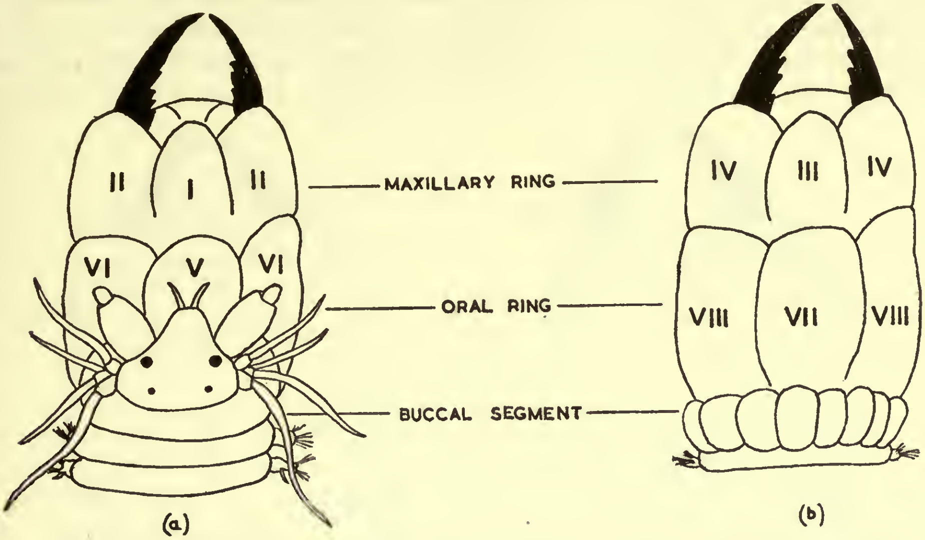

FIG. 6. Diagrammatic representation of the division of the proboscis in Nereidae.

KEY TO GENERA

1.	Horny paragnaths of one type only, conical	*Nereis.*
	Horny paragnaths of more than one type	2.
2.	Horny paragnaths of two types, conical teeth and transverse cutting plates .	*Perinereis.*
	Horny paragnaths of three types, conical, transverse and pectinate .	*Pseudonereis.*

Genus *NEREIS* Linnaeus, 1758

All groups of paragnaths complete—*Neanthes*, sub-genus.
One or more groups of paragnaths missing—*Nereis, sensu strictu.*

Nereis falsa Quatrefages, 1865

Nereis callaona, Augener, 1918, pp. 184–186.
Nereis falsa, Fauvel, 1923, pp. 337–338, fig. 129, *e–m*.
Nereis falsa, Day, 1951, pp. 27–28.

LOCALITIES. (1) Tenpobo shore (3), anterior pieces only, 11–15 mm. long. (2) (*a*) Accra, Christiansborg shore, 17.iii.49 (20 +), many complete, between 30–60 mm. long; (*b*) Accra, on sponge near Sound, 9.xii.50 (1), anterior fragment 10 mm. long; (*c*) from wood netted off Chorkor, 14.v.51 (1), complete, 18 mm. long. (3) (*a*) Winneba shore (1), anterior fragment, 10 mm. long; (*b*) Winneba, neap tide, 15.xi.49 (3), 20–30 mm. long. (4) Axim, (*a*) Shore 13/14.iv.49 (4), 2 complete, 50 mm. long, others anterior fragments, 10–15 mm. long; (*b*) Hospital Reef, 7.i.51

(9), some complete, 10–15 mm. long; (*c*) Lighthouse Reef, 8.i.51 (2), complete 10 and 20 mm. long.

This is one of the commonest littoral forms of the area. The arrangement of the paragnaths varies very little from that shown in Text-fig. 7, though paired groups VI sometimes have three or five teeth instead of two sets of four; area V never has any paragnaths. Notopodial chaetae are homogomph spinigers throughout, except that in some of the posterior feet a single homogomph falciger may be present (Text-fig. 8, *a*). Neuropodia have homogomph spinigers and heterogomph falcigers dorsally and heterogomph spinigers (Text-fig. 8, *b*) and falcigers ventrally.

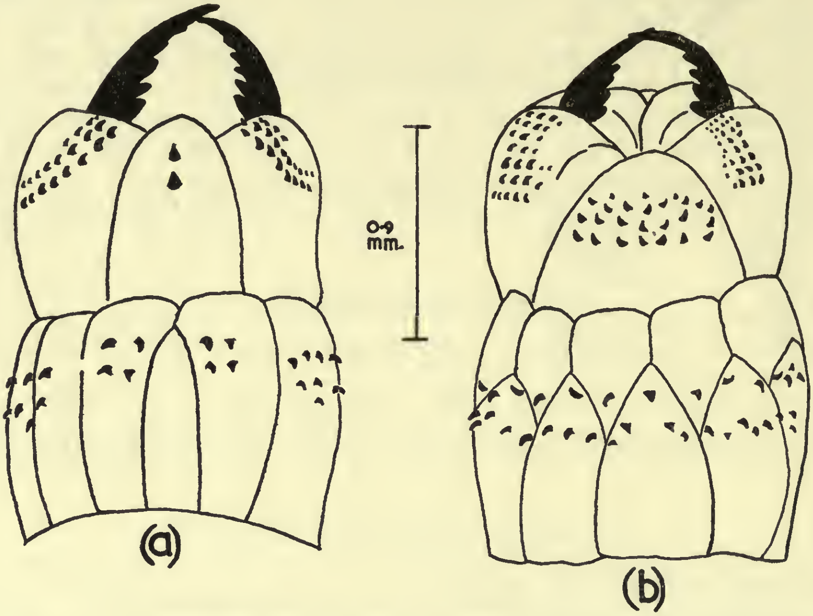

FIG. 7. *Nereis falsa*. Arrangement of the paragnaths on the proboscis, (*a*) dorsal; (*b*) ventral. (Specimen from Tenpobo.)

DISTRIBUTION.—Atlantic, Mediterranean, Adriatic and around the South African coast from Cape Town to Natal.

Nereis (Neanthes) succinea (Frey & Leuckart), 1847

Nereis glandulosa, Augener, 1918, pp. 192–194.
Nereis succinea Fauvel, 1936, pp. 307–313, (*nec Nereis succinea* Fauvel, 1923, pp. 346–347.)

LOCALITIES. Off Accra: (*a*) From wood netted of Chorkor, in 14 metres, 14.v.51 (3), complete, 11–25 mm. long; (*b*) Stn. 29 (1), complete, 25 mm. long; (*c*) 12 metres off Accra (1), 38 mm. almost complete; (*d*) Buchanan Survey, in a depth of 3·6 to 11·0 metres (10), between 25–60 mm. long, one a heteronereis.

The pattern of paragnaths varies considerably in this species around a typical form shown in Text-fig. 9. Thus I =1–4 in a longitudinal line; II = arcs in two rather scattered rows; III = a transverse group in 2–3 scattered rows; IV = arced masses; V = 0–4 (rarely 5–7). The absence of teeth on V in four of the specimens from the Buchanan Survey does not necessarily upset the validity of the above key, since this may be due to immaturity, accidental loss, general wear and tear, or it may indicate the approach of sexual maturity. This latter reason is of doubtful significance, but is referred to because this group is missing in the heteronereis example. Area VI is typically described as having a circle of six to seven paragnaths surrounding a central one, but the majority of specimens here examined conform to the pattern shown in Text-fig. 9, in which between 9–13 teeth are arranged in three scattered rows. A specimen in the B.M. (N.H.), Reg. No. 1928.4.26.290, from French Guinea, identified by Professor Fauvel, has 9–10 teeth in three scattered rows, and this variation may be common among W. African examples of *N. succinea*. Teeth in areas VII and VIII are both small and large and arranged, approximately, in two rows.

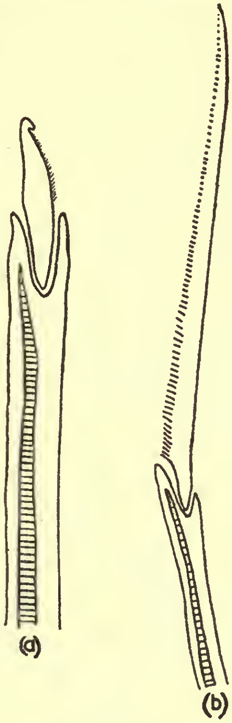

FIG. 8. *Nereis falsa*. (*a*) Homogomph falciger from a posterior notopodium, (*b*) heterogomph spiniger from a neuropodium. Both × 250. (Specimen from Axim.)

A parapodium from the posterior region of one specimen is shown in Text-fig. 10. The enlargement of the dorsal lobe only takes place posteriorly, anteriorly it is long and thin. Notopodial chaetae are homogomph spinigers, neuropodial chaetae

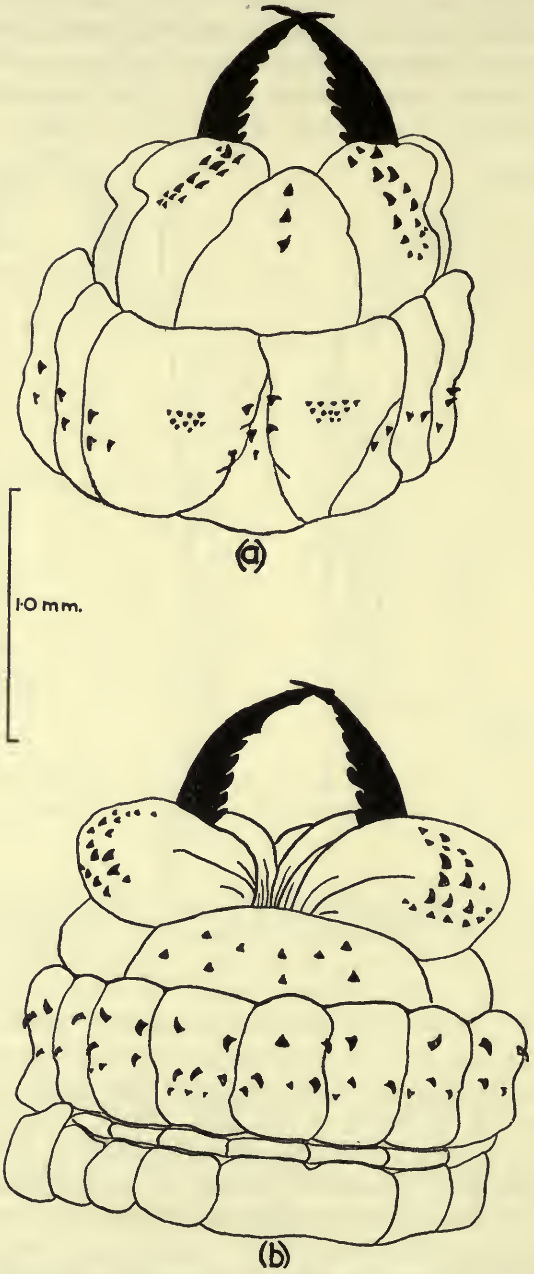

FIG. 9. *Nereis succinea.* Arrangement of the paragnaths on the proboscis, (*a*) dorsal, (*b*) ventral. (Specimen from the Buchanan Survey.)

homogomph spinigers, and heterogomph spinigers and falcigers. The absence of notopodial homogomph falcigers is considered by many workers (Fauvel, 1936; Hartman, 1951) to be important diagnostically. It is doubtful if a negative character of this type can be so considered, since accidental loss of chaetae frequently occurs.

DISTRIBUTION. Cosmopolitan; frequently found in waters of low salinity.

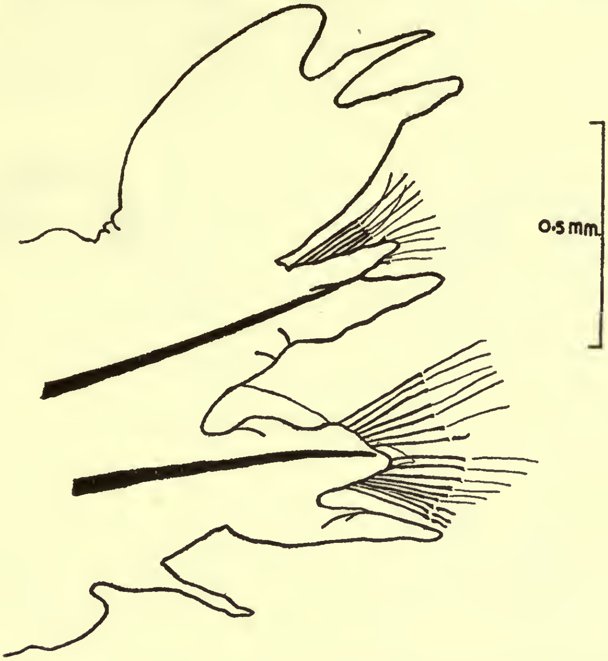

FIG. 10. *Nereis succinea.* Posterior view of parapodium from the 32nd chaetiger. (Specimen from the Buchanan Survey.)

Genus *PERINEREIS* Kinberg, 1865

With transverse chitinous plates (horny paragnaths) on area VI; other areas with conical paragnaths.

Perinereis melanocephala McIntosh, 1885

Nereis (*Perinereis*) *melanocephala*, McIntosh, 1885, pp. 216–219, pl. 34 figs. 14–17; pl. 16A, figs. 8, 9; from Bermuda, between tide marks.

Nereis (*Perinereis*) *melanocephala*, Augener, 1918, pp. 209–212, from the Island of Annobon and the Cameroons.

LOCALITIES. (1) Tenpobo shore (8), 6 complete, 20–30 mm. long, others ant. fragments: collected February, 1950. (2) Accra, Christiansborg shore (1), ant. piece 38 mm. long. (3) Winneba shore, 15.xi.49, Neap tides (2), anterior pieces, 17–20 mm. long—one a developing heteroneis stage. (4) Sekondi, high level plateau, 21.ii.49 (3) complete, 20–25 mm. long. (5) Dixcove shore (1), complete, 64 mm. long. (6) Axim, 13/14.iv.49 (1), complete, 18 mm. long.

The proboscis of this species is shown in Text-fig. 11. Little variation from the normal has been found; I = a triangular area of teeth; II = rhomboidal area of similar size to I; III = rectangular area also equal to I; IV similar to II; V = a single large tooth; VI = single long, transverse, horny bands; VII and VIII = 2 rows of teeth with scattered isolated teeth here and there. This compares accurately with McIntosh's original description. Unfortunately the type specimen, B.M. (N.H.). Reg. No. 1885.12.1.159 has no head. Efforts to find this portion, including enquiries at the University of St. Andrews, where McIntosh did his work, have been unsuccessful. Notopodial chaetae are all homogomph spinigers (Text-fig. 12, *b*), as are the superior neuropodial group. Inferior neuropodial chaetae are heterogomph falcigers (Text-fig. 12, *a*). The superior notopodial lobe becomes enlarged in the region of the 37th foot, continuing thus to the end of the body, the dorsal cirrus being attached (Text-fig. 13, *a*) to its indented extremity. The degree of this enlargement may be noted with respect to an anterior foot illustrated in Text-fig. 13, *b*.

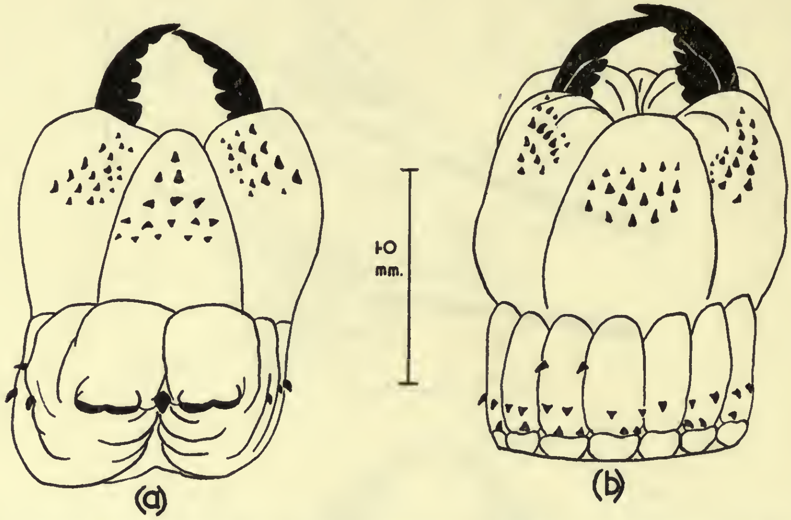

FIG. 11. *Perinereis melanocephala*. Arrangement of the paragnaths on the proboscis, (*a*) dorsal, (*b*) ventral. (Specimen from Sekondi.)

One of the specimens from Winneba has modified parapodia, beginning at the 17th segment, indicating the development of the heteronereis stage (Text-fig. 14). The lobe at the base of the dorsal cirrus, the post-chaetal neuropodial lobe and the ventral cirrus are all in the early stages of development into foliaceous swimming surfaces. The chaetae, however, remain normal, not having developed into the natatory type expected in this genus, otherwise the aspect of the parapodia is similar to that assumed by the more common *P. cultrifera* in the heteronereis condition.

DISTRIBUTION. *P. melanocephala* is only known from the above records.

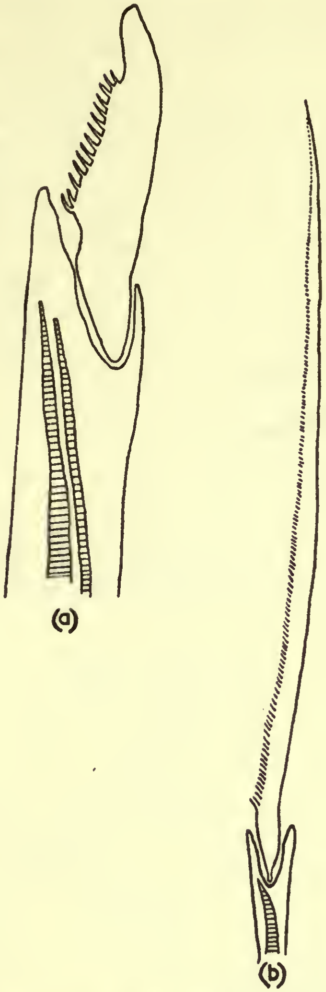

FIG. 12. *Perinereis melanocephala*. (*a*) Neuropodial heterogomph falciger, × 500; (*b*) notopodial homogomph spiniger, × 250. (Specimen from Sekondi.)

Genus ***PSEUDONEREIS*** Kinberg, 1865

With transverse chitinous plates (horny paragnaths) on area VI; transverse rows of pectinate teeth and conical paragnaths on other areas.

Pseudonereis gallapagensis Kinberg, 1865

Pseudonereis gallapagensis, Gravier, 1909, pp. 629–633, figs.
Pseudonereis variegata, Fauvel, 1927b, pp. 527–528, (part).
Pseudonereis gallapagensis, Hartman, 1948, pp. 68–69.

LOCALITIES. (1) (*a*) Winneba shore, 3.iii.50 (1), complete, 9 mm. long, 4.iii.50 (2), one complete, 15 mm.; (*b*) Winneba rock face, 22.xi.49 (6), several complete,

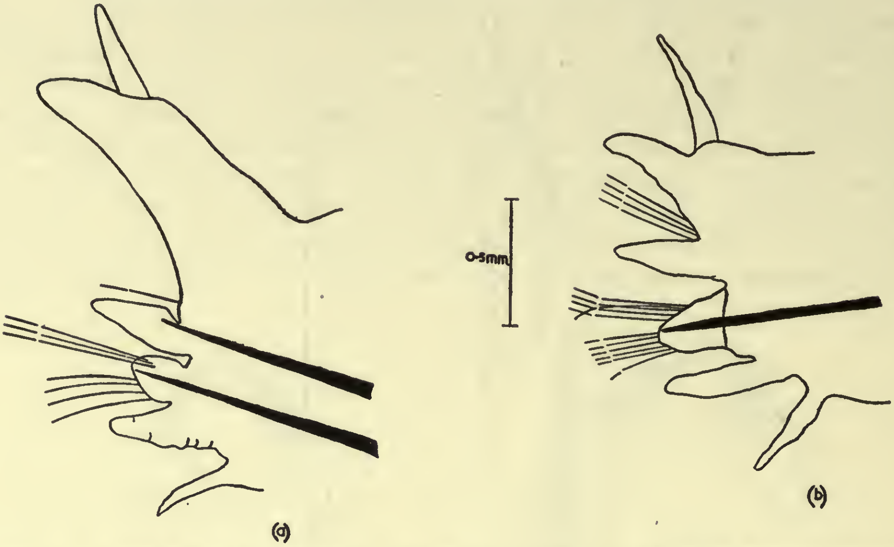

FIG. 13. *Perinereis melanocephala.* Parapodia of (*a*) 37th chaetiger (specimen from Sekondi) ; (*b*) an anterior chaetiger (specimen from Tenpobo).

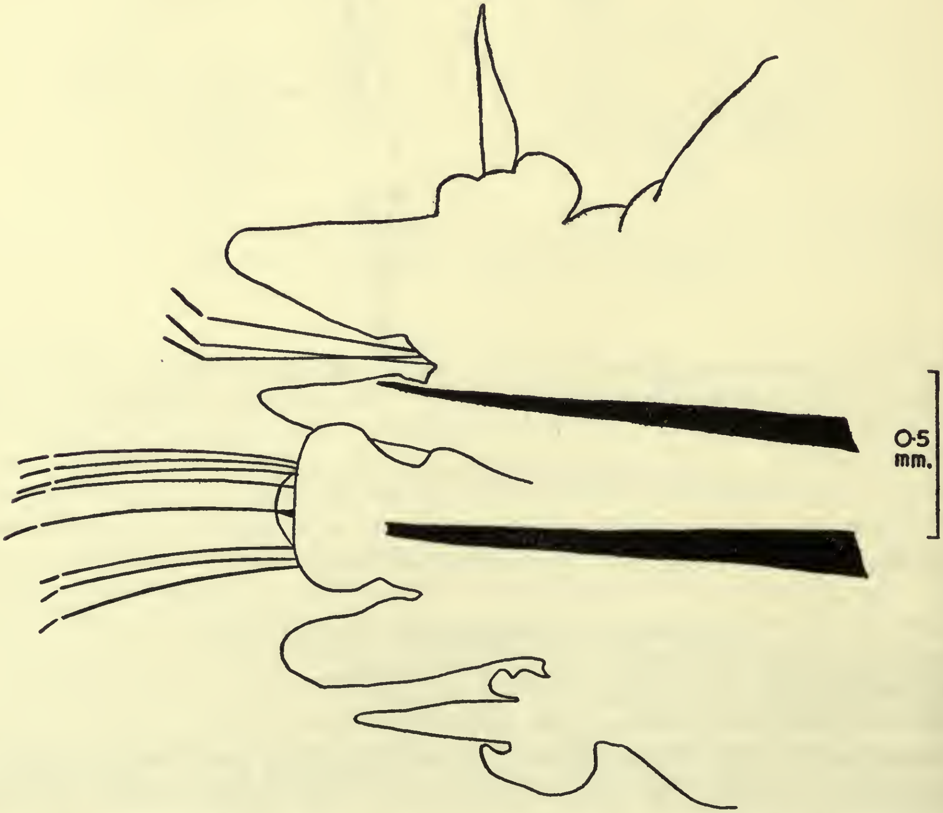

FIG. 14. *Perinereis melanocephala.* Parapodium from the 23rd chaetiger of a developing heteronereid. (Specimen from Winneba.)

between 15–30 mm. long; (2) (*a*) Axim shore, 13/14.iv.49 (1) complete, 19 mm. long; (*b*) Axim, hospital reef (2), both complete, one approaching sexual maturity, 17 mm. long, the other 11 mm. long.

Notopodial chaetae are homogomph spinigers; superior neuropodial chaetae also homogomph spinigers, whilst the inferior group are heterogomph falcigers. Posteriorly the dorsal lobe becomes foliaceous and carries at its distal end the dorsal cirrus, leaving little or no free margin. Hartman (1948) referred to this character as the specific distinction between *P. gallapagensis* and *P. variegata* (Grube), noting that the latter species had a free portion at the tip of the dorsal foliaceous lobe. Day (1951) disputed the value of this distinction and it is doubtful if it is of practical use. It is here suggested that *P. gallapagensis* has on each area IV of the proboscis an apical group of about 16 small conical teeth in addition to the rows of pectinae (Text-fig. 15, *c*), and this is a diagnostic character separating it from *P. variegata*. Kinberg (1865) did not note this character, though his figures were not drawn in a position which would show it. In examining the type specimen, which was in poor condition, Hartman (1948) did not refer to the proboscidean structures. Gravier (1909), however, observed this apical group on IV in specimens collected from Peru.

In groups VII and VIII in *P. gallapagensis* there is one row of alternating long and short teeth (Text-fig. 15, *b*), the anterior tip of the long teeth being in line with the latter. This is the condition on an extruded proboscis. If not extruded, however, due to the different lengths of alternate teeth, and the general contracted condition of the proboscis, it appears as if two rows of teeth are present. This character is clearly shown in Kinberg's (1910) type figure and contrasts with the condition in *P. variegata* in which there are 2/3 rows of short teeth (McIntosh, 1903). All speci-

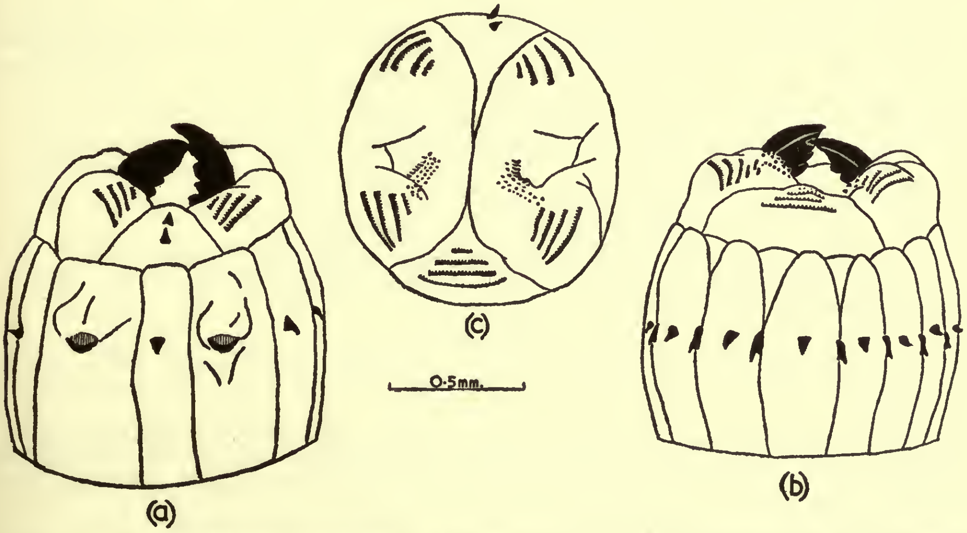

FIG. 15. *Pseudonereis gallapagensis*. Arrangement of the paragnaths on the proboscis, (*a*) dorsal, (*b*) ventral, (*c*) apical (jaws left out). (Specimen from Axim.)

mens here listed agree with this description, as does one from the Cameroons in the B.M. (N.H.), Reg. No. 1928.4.2.844, which was recorded by Fauvel, 1927*b*, as *P. variegata*. Further specimens of *P. gallapagensis* in the B.M. (N.H.) collections come from Ceylon and from Mormugas Bay, Goa, near Bombay.

Distribution. This is the first record of this species from the W. African coast; apart from the above records, *P. gallapagensis* is known widely from the western coast of S. America, the Galapagos Islands and Hawaii.

Family Nephthydidae

Body with numerous short segments. Prostomium small and flat carrying two pairs of antennae. Proboscis terminated with 14 to 22 soft bifid papillae and bearing 14 to 22 longitudinal rows of similar processes externally and two horny jaw pieces on its inner wall. Parapodia are biramous except for the first pair which may not be fully developed; rami are wide apart with a coiled cirrus, probably branchiate in function, between them.

Only three genera are recognized in this family and the following key has been adapted from Hartman (1950) in which work an acceptable division of the type genus *Nephthys* was suggested:

1. Inter-ramal cirri (branchiae) recurved—evolute . . . . *Nephthys.*
2. „ „ „ involute . . . . *Aglaophamus.*
3. „ „ „ absent . . . . *Micronephthys.*

No examples of the genus *Micronephthys* Freidrich, 1939, have been collected from the Gold Coast, but Augener (1918) recorded *M. ambrizettana* from Angola.

Genus *NEPHTHYS* Cuvier, 1817

Nephthys hombergii Audouin & Milne-Edwards, 1830

Nephthys hombergii, Fauvel, 1923, p. 367, fig. 143, *a–d*.

Localities. Off Accra: Stn. 71 (1) 12 mm. long, anterior piece; Stn. 132 (1) 16 mm. long, anterior piece; Buchanan Survey, in 3·5 to 11 metres (2), one complete, 54 mm. long.

This well-known species is characterized by 22 longitudinal rows of papillae on the proboscis, the appearance of the branchiae on the 4th chaetiger and the presence of a notopodial button ventral to the acicula and tending to overgrow it.

Distribution. North Sea, English Channel, Mediterranean, Atlantic.

Genus *AGLAOPHAMUS* Kinberg, 1865

Aglaophamus lyrochaetus (Fauvel), 1902

Nephthys lyrochaeta Fauvel, 1902, pp. 72–5, figs. 9–12, from the estuary of the R. Casamance, Senegal.

Nephthys lyrochaeta, Augener, 1918, pp. 160–166, pl. 2, fig. 12; pl. 3, fig. 59, from Saltpond, Gold Coast in 9 metres, and Accra; also several other W. African stations.

LOCALITIES. Off Accra: Stn. 32 (1), anterior piece, 10 mm. long; Stn. 59 (1), anterior piece, 7 mm. long; Stn. 70 (2), both anterior pieces, 7 and 8 mm. long; Buchanan Survey, in 3·5–11 metres depth (4), two complete, 26 and 28 mm. long.

There are 14 longitudinal rows of papillae on the proboscis in this species. The "lyre" bristles occur in the centre of each group of chaetae and are about half the length of the others. They are therefore difficult to see unless the parapodium chosen for observation is carefully mounted. A later diagnosis by Fauvel (1927*b*) of *A. lyrochaetus* indicated the presence of a small lobe on the dorsum of the neuropodium which was confirmed by Monro (1930). With the "lyre" bristles, this character serves as specifically diagnostic. The anterior feet are biramous and not uniramous as indicated by Augener (1918), and the long ventral and dorsal cirri of the first and second chaetigers respectively, noted by Monro (1930), are not present in the specimens here described.

DISTRIBUTION.—*A. lyrochaetus* is only known through the above records.

Family GLYCERIDAE

Body elongate, tapering to both extremities, segments bi- or triannulate. Prostomium conical, annulated, with four small terminal antennae. Protrusible proboscis, very long, covered with papillae and armed with horny jaws of various kinds. Normally with biramous parapodia, but frequently uniramous anteriorly. Branchiae, when present, compound or simple, often retractile. Chaetae simple or compound.

KEY TO SUBFAMILIES

1. Body divided into 2 or 3 regions by variation in the form of the parapodia which may be uniramous, sub-biramous or biramous. Jaws and paragnaths numerous GONIADINAE.
2. Body not divided into distinct regions, parapodia either uniramous or biramous throughout. Jaws and paragnaths few in number . . . . GLYCERINAE.

Subfamily GLYCERINAE

KEY TO GENERA

1. Parapodia uniramous throughout, with compound cheatae only . . *Hemipodus*.[1]
2. Parapodia biramous throughout, with simple chaetae in notopodia and compound chaetae in neuropodia . . . . *Glycera*.

[1] Not recorded from the Gold Coast.

Genus *GLYCERA* Savigny, 1818

Prostomium long, with more than three annulations. Proboscis with four large horny paragnaths distally and covered with papillae. Parapodia with a stumpy dorsal cirrus, two anterior lobes one or two posterior lobes and a ventral cirrus. Neuropodial chaetae compound spinigers, notopodial chaetae simple capillaries. Branchiae present or absent, simple or branched, permanent or retractile into the foot.

Glycera convoluta Keferstein, 1862

Glycera africana, Arwidsson, 1898, pp. 21–22, pl. 1, figs. 10–12.
Glycera africana, Augener, 1918, pp. 384–386.
Glycera tridactyla, Augener, 1918, pp. 386–389, pl. 5, figs. 142–143, text-fig. 47.
Glycera convoluta, Fauvel, 1923, pp. 383–385, fig. 150, *a–h*.

LOCALITIES. (1) Off Accra: Stn. 65 (1); Stn. 69 (1); Stn. 89 (1); Stn. 126 (1); all incomplete except Stn. 65, which measures 55 mm. long; Buchanan Survey in 3·6 to 11·0 metres depth (6), five complete, 40–52 mm. in length. (2) Apam shore, 3/4.iv.50 (3), one complete, 46 mm. long.

The papillae of this species are illustrated in Text-fig. 16, *a* and *b*. They are cylindrical with a truncated termination, the truncation bearing a plate similar in appearance to the nail on the human finger. Over the greater part of the body both anterior parapodial lobes are bluntly pointed and each project the same distance from the body; posterior lobes are unequal, the dorsal being blunt to oval and projecting a short distance, whilst the ventral lobe is blunt and hardly projects at all. Branchiae are non-retractile and lie on the dorsal edge of the parapodia. In the anterior region they project as far as the chaetae, but posteriorly become very much longer. Normally the branchiae appear at the 14th–18th parapodia, but they may not appear until the 29th foot. They are absent from extreme posterior segments.

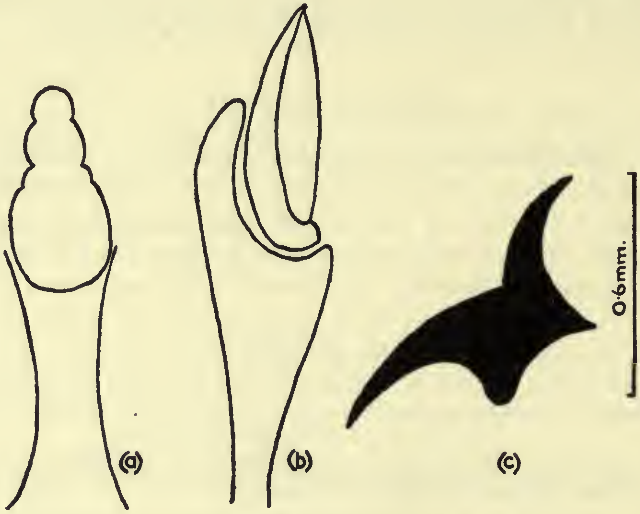

FIG. 16. *Glycera convoluta*. (*a*) Papilla from the proboscis, *en face* view, × 1500 (specimen from Apam); (*b*) papilla from the proboscis, side view, × 1500 (specimen from Stn. 89); (*c*) silhouette of one of the 4 jaw articles, drawn *in situ*, (specimen from Stn. 126).

A silhouette of one of the paragnaths is shown in Text-fig. 16, *c*, it was drawn *in situ*, at the end of the protruded proboscis.

DISTRIBUTION. Mediterranean Sea and Atlantic Ocean.

Subfamily GONIADINAE

KEY TO GENERA

1.	Proboscis with chevrons	*Goniada*.
	Proboscis without chevrons	2.
2.	Neuropodia with spinigerous chaetae only	*Ophioglycera*.
	Neuropodia with spinigerous and falcigerous chaetae	*Goniadopsis*.

Genus ***GONIADA*** Audouin & Milne-Edwards, 1833

Body divided normally into two regions, an anterior uniramous and a posterior biramous portion ; there may be a transitional region with sub-biramous parapodia. Paragnaths include a pair of large dentate macrognaths separated from each other by dorsal and ventral arcs of micrognaths. The proboscis carries two rows of dark hard V shaped pieces, chevrons, and numerous papillae of one or few kinds, distributed in longitudinal, or irregular bands.

Goniada multidentata Arwidsson, 1899

Goniada multidentata Arwidsson, 1898, pp. 45–47, figs. 40–42.

LOCALITY. Off Accra, Buchanan Survey in 39·6 metres depth, off Lagoon (1), complete, about 90 mm. long.

There are 36 anterior uniramous, 15 median sub-biramous, and 131 posterior biramous, parapodia. The uniramous feet bear prominent thick ventral cirri and slender pointed dorsal cirri. There are three ligules to each chaetigerous lobe, two anterior, long and finger-shaped, and one posterior, short. The sub-biramous portion is so qualified only because the notopodial lobes are not well developed and also because the segments in this region are the same width as those in the anterior uniramous region. Notopodial chaetae, however, are developed and the segments are strictly biramous. In the biramous posterior portion the segments are much wider than anteriorly. Neuropodial ligules are as in the anterior region except that the posterior ligule is triangular ; there are two notopodial ligules, both blunt, one dorsal and the other ventral to the chaetae. Notopodial chaetae are acicular. Neuropodial chaetae and chaetae in the anterior uniramous part are long heterogomph spinigers (Text-fig. 17, *a*).

The large macrognaths each carry 12 teeth, six large and six small. There are 30 dorsal and 12 ventral micrognaths. Papillae from the proboscis are illustrated in Text-fig. 17, *b*. About 150 pairs of chevrons have been counted, extending in two rows along almost the full length of the proboscis. Arwidsson reported 90 pairs in his original description, but it is not considered that the extra number present in the Accra specimen is sufficient to warrant specific distinction. In all other characters the specimens appear to be identical, and since the Accra specimen is almost twice as long as Arwidsson's the variation may be taken to indicate differences in growth stages.

DISTRIBUTION. This species is known only from the tropical coast of West Africa.

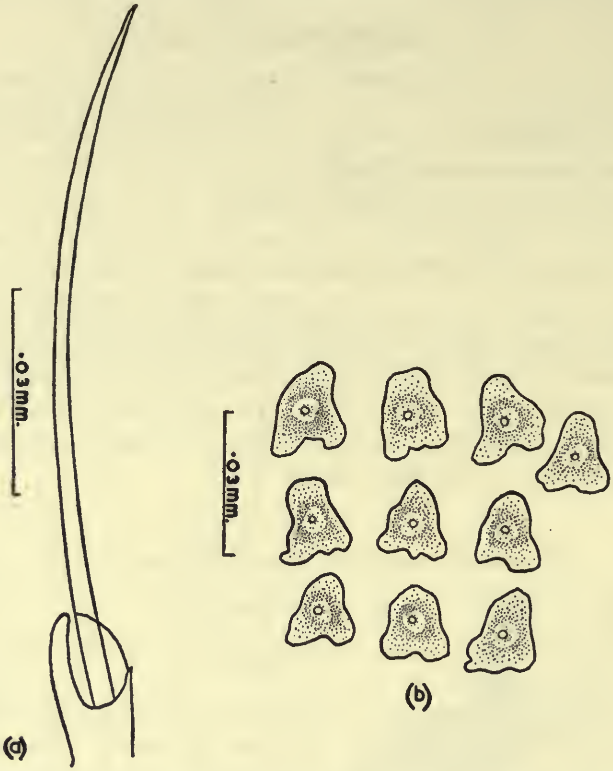

FIG. 17. *Goniada multidentata.* (*a*) Chaeta from the anterior uniramous region ; (*b*) group of papillae from the proboscis.

Genus *GONIADOPSIS* Fauvel, 1928

Body divided into three distinct regions ; (1) anterior, with uniramous parapodia and stout falcigerous chaetae ; (2) median, with uniramous parapodia and spinigerous chaetae ; (3) posterior, with biramous parapodia, notopodial acicular chaetae and long spinigerous neuropodial chaeta. Papillae on the proboscis are numerous, of one or few kinds.

Goniadopsis incerta Fauvel, 1932

Goniada (*Goniadopsis*) *incerta* Fauvel, 1932, pp. 122–123, pl. 4, figs. 1–10, from Akyab, Burma.
Goniadopsis incerta, Day, 1953, p. 430, from the estuary of the Zwartkops River, Cape Province, South Africa.

LOCALITY. (1) Apam shore, 4.iv.50 (1), 35 mm. long.

The anterior region consists of 33 segments. Parapodia have three ligules, two anterior, finger shaped, of equal length, one posterior, broad and triangular. One of the stout falcigerous chaetae is shown in Text-fig. 18, *a*. Ventral cirri are short and blunt anteriorly, but elongate in the posterior segments of this region.

The median region consists of 37 segments. Parapodial ligules are similar to those in the anterior region. One of the compound spinigers is shown in Text-fig. 18, *b*. Ventral cirri are very long, dorsal cirri are short.

The posterior biramous portion makes up the remainder of the body of 111 segments. There are two notopodial ligules, one posterior; neuropodial ligules are similar to those in the anterior region except that the posterior one is drawn out to a blunt point. Compound spinigers are as in the median region.

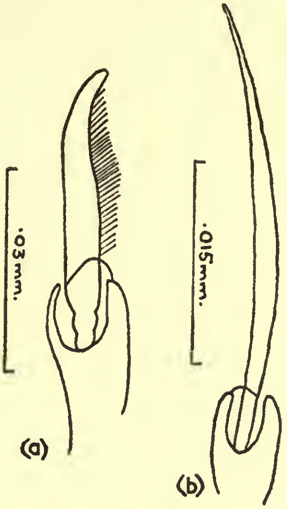

FIG. 18. *Goniadopsis incerta.* (*a*) Falciger from the anterior region; (*b*) spiniger from the median region.

There is one pair of small eye-spots at the base of the annulated prostomium.

DISTRIBUTION. This is the first record of this genus from the Atlantic Ocean.

Genus ***OPHIOGLYCERA*** Verrill, 1885

Body divided into three regions; (1) anterior with uniramous parapodia, with spinigerous chaetae; (2) median, in which notopodia with simple chaetae are gradually developed; (3) posterior, with biramous parapodia. Proboscis long, terminated with a circlet of soft fleshy papillae, within which is a circlet of macrognaths. Papillae on the proboscis are numerous of one or few kinds.

Ophioglycera archeri sp. n.

Holotype, B.M. (N.H.), Reg. No. 1953.3.1. 648.

LOCALITY. Off Accra, Buchanan Survey, in 7·3 metres off Castle (1), complete, 134 mm. long. The proboscis, which is not protruded, measures about 25 mm. long.

The prostomium is without visible annulations or eye-spots. Eighteen large papillae form a crown at the end of the proboscis. The proboscideal teeth form a circlet, adjacent to the papillae, of two large separate macrognaths having between them groups of 18 and 25 micrognaths. The macrognaths have four teeth each, two large and two small, the micrognaths are bidentate. Papillae cover the surface of the proboscis and appear to be all alike (Text-fig. 20, *b*).

On the first foot there is a single cirrus with no chaetae. Thereafter there are 27 uniramous parapodia with spinigerous chaetae (Text-fig. 19, *a*), 49 segments in which notopodia are developed, but in which the rami are close together (Text-fig. 19, *b*) and 140 biramous parapodia in which the rami are far apart (Text-fig. 20, *a*). Neuropodial chaetae are compound spinigers throughout, notopodial chaetae are simple.

In this specimen biramous parapodia are not gradually developed. At the 28th chaetiger the notopodial ramis appear fully developed with lobes and simple chaetae. A third division of the body, however, is recognizable at the 77th chaetiger where notopodia and neuropodia are much wider apart than they are anteriorly, and the chaetigerous ligules are much more foliaceous (compare Text-fig. 19, *a* and 19, *b* with Text-fig. 20, *a*).

No diagnostic coloration is apparent in the preserved condition of the worm.

No other species of *Ophioglycera* is known in which the change in form of the parapodia begins as far forward as in *O. archeri*. In *O. foliocea* the change begins at about the 35th chaetiger, but in *O. longicirrata*, *O. gigantea*, *O. eximia* and *O. distorta* it does not appear until the 55th or 59th, and, exceptionally, may be delayed to the 90th.

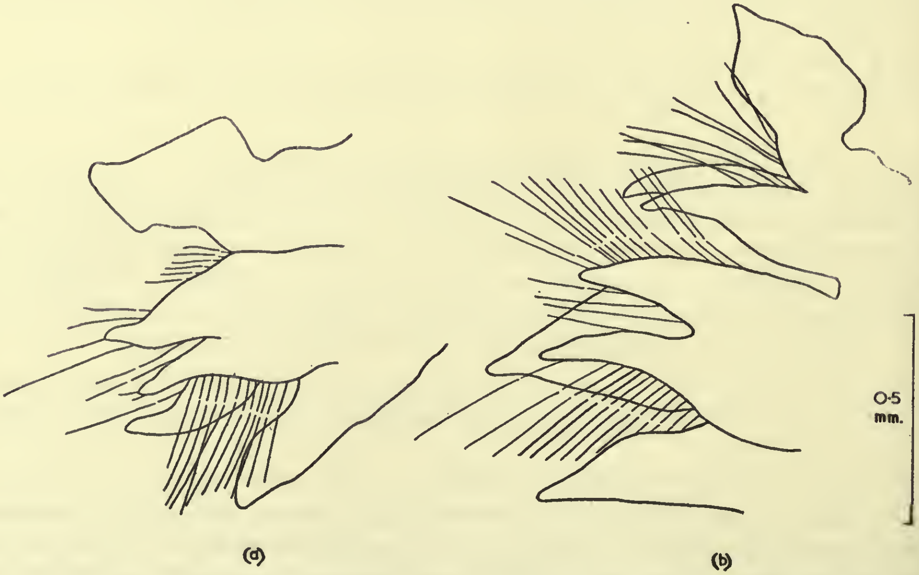

FIG. 19. *Ophioglycera archeri*, sp. n. Parapodia, (*a*) 13th foot, (*b*) 28th foot.

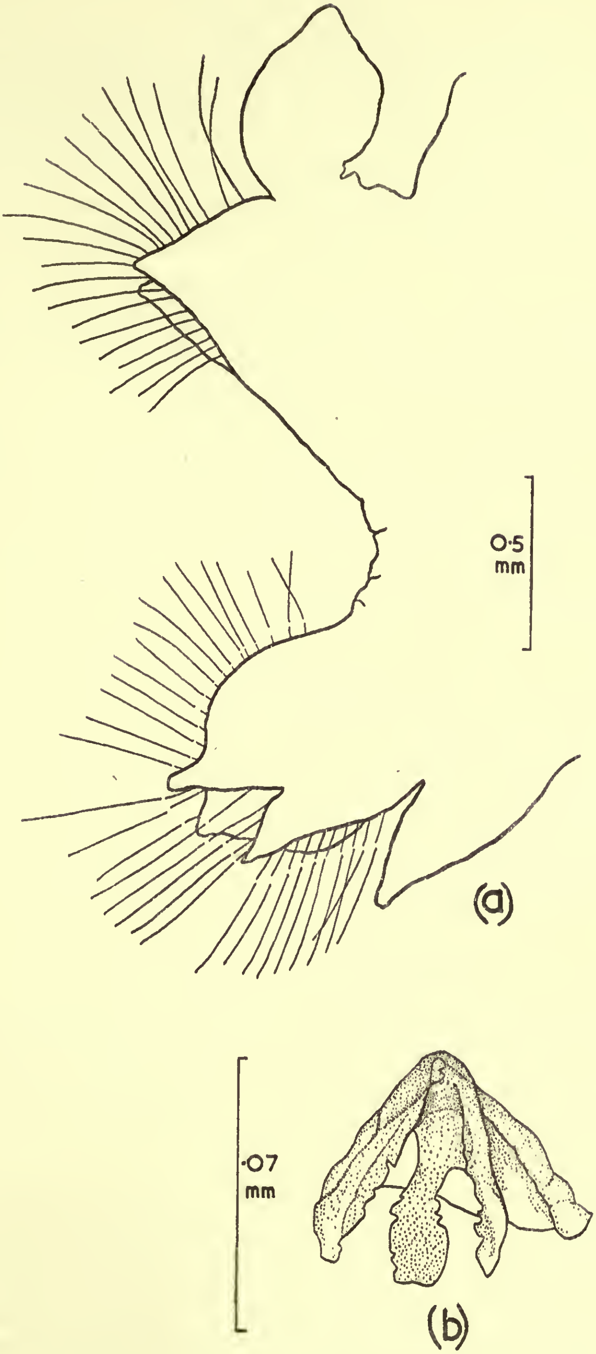

Fig. 20. *Ophioglycera archeri*, sp. n. (*a*) Parapodium from a posterior foot of a mature ♀; (*b*) papilla from the proboscis.

Family EUNICIDAE

Body elongated, with the prostomium normally having one pair of palps and one to seven antennae. First two segments normally achaetous and apodous. Sometimes one pair of tentacular cirri on the 2nd segment. Parapodia uniramous or sesquiramous. Dorsal cirrus, with or without branchiae, sometimes missing or rudimentary; ventral cirrus often absent. Chaetae simple and/or compound, showing great variety of shape. Proboscis armed with a ventral mandible and dorsal maxillae. A membranous tube is secreted by some species.

KEY TO SUB-FAMILIES

1.	Prostomium reduced, without appendages (except in *Augenaria* Monro, with three minute antennae). No ventral cirri; dorsal cirri rudimentary	LUMBRINERINAE.
	Prostomium with appendages, palps and antennae	*2.*
2.	No ventral cirri; dorsal cirri foliaceous. Three antennae	LYSARETINAE.
	Ventral cirri present	*3.*
3.	Two antennae. Maxillae of two or four longitudinal series of very small and numerous pieces	DORVILLEINAE.[1]
	One to seven antennae. Maxillae of four or five pairs of pieces	*4.*
4.	Seven antennae, five occipitals mounted on ringed ceratophores and two ovate frontals	ONUPHIDINAE.
	One to five antennae, ovate frontals absent	EUNICINAE.

Sub-family EUNICINAE

KEY TO GENERA

1.	Branchiae present. Five antennae	*2.*
	Branchiae absent	*3.*
2.	Tentacular cirri present	*Eunice.*
	Tentacular cirri absent	*Marphysa.*
3.	Three tentacles, tentacular cirri absent	*Lysidice.*
	One tentacle, tentacular cirri present	*Nematonereis.*[1]

Genus *EUNICE* Cuvier, 1817

Five antennae. One pair of tentacular cirri on the second apodous segment. Dorsal cirri elongated, ventral cirri short or knob-like. Branchiae simple or pinnate. Parapodia sesquiramous, with acicular chaetae. Simple pectinate (comb-like) chaetae, and compound chaetae. Mandible of two pieces. Maxillae with a pair of forceps and two or three pairs of toothed plates, an unpaired left plate and sometimes paragnaths.

There are manifold difficulties in identifying incomplete specimens of *Eunice*. The most important of these concerns the arrangement of those characters which appear on every parapodium, thus necessitating complete specimens for accurate diagnosis. A high degree of variability in the arrangement of branchiae, jaw plate dentition and extent of antennal annulation within any one species introduces further uncertainty. For these reasons all specific identifications of incomplete specimens are doubtful.

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[1] Not recorded from the Gold Coast.

KEY TO SPECIES

1. Branchiae normally absent; when present, simple, posterior, with one filament, sometimes 2–3 . . . . . *E. gracilis.*
   Branchiae, always present, pinnate . . . . . *2.*
2. Subacicular hooks bidentate . . . . . *3.*
   Subacicular hooks tridentate . . . . . *4.*
3. Branchiae occur only on the anterior part of the body beginning at about the 6th chaetiger . . . . . *E. coccinea.*
   Branchiae occur only on the middle and posterior part of the body, beginning at about the 26th chaetiger . . . . . *E. filamentosa.*
4. Branchiae first present from about the 3rd chaetiger but absent over the greater part of the body from the middle backwards . . . . . *E. vittata*
   Branchiae first present from the 3rd to 7th chaetigers, and also present over the greater part of the posterior region . . . . . *5.*
5. Branchiae present on the last few chaetigers . . . . . *E. antennata.*
   Branchiae absent from the last few chaetigers . . . . . *E. rubra.*

Eunice antennata Savigny, 1818

Eunice antennata, Crossland, 1904, pp. 312–318, figs. 56–60.
Eunice antennata, Hartman, 1944*a*, pp. 115–117, pl. 7, figs. 154–156.

LOCALITIES. (1) Tenpobo shore, (1), anterior fragment, 28 mm. long. (2) Off Accra, Dredge in 14·6 m., shingle, 2 miles south out from the R. Densu (1), 70 mm. long, complete, and several fragments.

The antennae are clearly annulated. Pectinate branchiae, in the dredged specimen, begin on the 7th chaetiger with 9 filaments; on the 24th, 32nd and 52nd feet there are 12, 4 and 1 filament to each gill respectively. An increase to 3 filaments then takes place, which is maintained up to the last three segments on all of which there is a further reduction to one. Subacicular hooks are tridentate, compound chaetae, bidentate falcigers; simple chaetae are capillary and pectinate. There are two pairs of anal cirri, one dorsal and long, the other ventral and short.

DISTRIBUTION. Cosmopolitan in tropical and subtropical areas.

Eunice vittata (Delle Chiaje), 1829

Eunice vittata, Augener, 1918, pp. 321–323.
Eunice vittata, Fauvel, 1923, pp. 404–405, fig. 158, *h–n.*
Eunice vittata, Hartman, 1944*a*, p. 118.

LOCALITIES. (1) Tenpobo shore, (1), ant. piece. (2) Off Accra: (*a*) Stn. 35 (1), complete, 14 mm. long; Stn. 47 (2), anterior pieces; Stn. 69 (1) anterior piece; Stn. 88 (1), complete, 8 mm. long; (*b*) Dredge in 14·6 m., shingle, 2 miles south out from the R. Densu (2), complete, 10 and 19 mm., long, and nine anterior pieces.

In the specimen from Stn. 88 branchiae appear on the 3rd chaetiger with three filaments. A maximum development of 7–8 filaments occurs on the 38th foot, after which there is a reduction to one and finally branchiae are missing entirely from the posterior segments. Subacicular hooks, and chaetae, are similar to those in *E. antennata.*

DISTRIBUTION. Mediterranean, Atlantic, and Pacific.

Eunice filamentosa Grube, 1857

Eunice filamentosa, Augener, 1918, pp. 324–327, from Pram Pram.
Eunice filamentosa, Hartman, 1944*a*, p. 107, pl. 6, figs. 123–126.

Localities. (*a*) Axim shore, 13/14.iv.49 (1), 40 mm. long, complete ; (*b*) Axim, Hospital Reef, 7.i.51 (1), 200 mm. long, complete.

In the specimen from Axim shore branchiae appear at the 29th chaetiger with one filament, gradually increase to a maximum of five and continue thus over the greater part of the body. Towards the pygidium there is a reduction to 3/4 filaments. The subacicular hooks which appear at the 23rd foot are strongly bidentate ; superior acicular have blunt, hammer-shaped ends.

The specimen from the Hospital Reef has branchiae appearing at the 26th chaetiger, the maximum number of filaments is five and this condition prevails over much of the body. There is again a gradual reduction in filament number towards the tail, but in this specimen it is carried much further, the last three chaetigers having no branchiae. Fragments of a papyraceous tube are present.

Distribution. Tropical West Africa, Eastern and Western Tropical America.

Eunice coccinea Grube, 1878

Eunice coccinea, Crossland, 1904, pp. 297–303, pl. 20, figs. 6, 7, text-figs. 46–51.
Eunice coccinea, Fauvel, 1932, p. 136.

Locality. Axim, Hospital Reef, 7.i.51 (2), one complete, 42 mm., one incomplete, 100 mm. long.

Branchiae begin on the 6th and 7th parapodia. They attain a maximum of 10–12 filaments in the anterior third and are missing throughout the rest of the body. Subacicular hooks appearing at the 25th and 28th feet, are bidentate.

Distribution. Frequently recorded in the tropical regions of the Atlantic and Indo-Pacific, from the Gulf of Guinea to the Philippines.

Eunice gracilis (Crossland), 1904

Nicidion gracilis, Crossland, 1904, pp. 327–329, pl. 22, figs. 10–11, text-figs. 65–66.
Eunice gracilis, Fauvel, 1932, pp. 140–141, text-fig. 20.
Eunice gracilis, Day, 1949, p. 447.

Localities. (1) Accra, (*a*) Christiansborg shore, 17.iii.49 (2), complete, 7 and 11 mm. long ; (*b*) Dredge 8 fathoms, shingle, 2 miles south of R. Densu (1), complete, 20 mm. long. (2) Dixcove, shore (10), five complete, 15–42 mm. long. (3) Axim, (*a*) Shore, 13/14.iv.49 (1), complete, 24 mm. long ; (*b*) Lighthouse Reef, 8.i.51 (1), complete, 20 mm. long ; (*c*) Hospital Reef, 13.iv.49 (1), complete, 22 mm. long ; 7.i.51 (10), seven complete, 10–18 mm. long.

Simple chaetae are capillaries and comb-like ; compound chaetae are bidendate. Subacicular chaetae appear at about the 25th foot and are also bidendate ; there is one to each parapodium compared with two in *E. cincta* Kinberg, (see Hartman, 1948, p. 80, on a re-examination of Kinberg's types). For this reason the synonymy proposed by Fauvel (1950) including *E. gracilis* as a synonym of *E. cincta* has not been accepted here. Antennae barely reach back to the 1st chaetiger; tentacular cirri have frequently been lost. No branchiae are present; anteriorly dorsal cirri are well-developed.

There has been much discussion about the generic status of this species. Originally designated a species of *Nicidion* because of the lack of branchiae, Fauvel (1932) and Day (1949) have reported gills sometimes present on extreme posterior segments, and for this reason the species is regarded as a *Eunice*.

DISTRIBUTION. Indian Ocean—Zanzibar, Gulf of Manaar, Mergui peninsular—and Atlantic Ocean. St. Helena and the Gold Coast.

Eunice rubra Grube, 1856

Eunice rubra, Augener, 1918, pp. 319–321, from Pram Pram, and the Island of Rolas, in the Gulf of Guinea.

This species has not been found in the present collections. The antennae are clearly annulated, branchiae begin at the 5th chaetiger and subacicular hooks are tridentate.

DISTRIBUTION. This species is common on the south-eastern coast of the U.S.A.

Genus ***MARPHYSA*** Quatrefages, 1865

Five antennae, two eyes. Tentacular cirri absent, dorsal cirri elongated; ventral cirri short. Branchiae simple or pectinate. Dorsal chaetae simple capillaries. Ventral chaetae simple or compound, comb chaetae, and acicular chaetae also present. Mandible of two pieces. Maxillae with a pair of forceps, two pairs of toothed plates, an unpaired plate and sometimes paragnaths.

Marphysa dartevellei Monro, 1936

Marphysa dartevellei Monro, 1936*b*, pp. 246–248, 6 figs, from the Congo coast, Cape Malemba, 85 km. north of Banana, from holes of *Lithodomus*.

LOCALITIES. (1) Tenpobo shore, 5.ii.50 (1), 325 mm. long, complete. (2) Accra, Christiansborg shore, 19.xi.49 (2), anterior pieces, 85 and 35 mm. long. (3) Axim, (*a*) Shore, 13/14.iv.49 (2), anterior pieces, 26 and 35 mm. long; (*b*) Hospital Reef, 7.i.51 (1), 58 mm. long, complete.

The antennae are unarticulated, equal in length, measuring only a little longer than the head; between the laterals there are two black eyes. Dorsal cirri are smooth and slender decreasing in length posteriorly. Ventral glandular pads are present after the first few chaetigers. Ventral cirri are well developed stumps in the anterior feet, but posteriorly become little more than tubercles at the top of the glandular pads. Pectinate branchiae begin between the 32nd to 40th chaetigers. They have a maximum of four to five filaments and are present over the greater part of the middle body region. In the complete specimen from Tenpobo there are 86 abranchiate segments posteriorly preceded by a large number of segments in which reduction to one filament has taken place.

In the anterior parapodia compound chaetae are spinigers and posteriorly are falcigers. Monro's original specimens were not complete and his suggestion that falcigerous compound chaetae replace spinigers posteriorly is here substantiated. Simple capillary chaetae occur throughout the body, simple comb-chaetae are present in the middle body region but are often difficult to find posteriorly.

There are two pairs of anal cirri, one pair elongated and dorsal, the other ventral and short.

DISTRIBUTION. This species is known only from the above records.

Genus ***LYSIDICE*** Lamarck, 1818

Three antennae. Tentacular cirri absent. Branchiae absent. Chaetae, simple capillaries, comb-like, compound falcigers and acicular. Mandible of two pieces. Maxillae with a pair of forceps, two toothed plates, an unpaired plate and paragnaths.

KEY TO SPECIES

1. Eyes round; antennae small, never reaching as far as the anterior border of the prostomium . . . . *L. ninetta.*
2. Eyes reniform; antennae reaching to the anterior border of the prostomium, sometimes further . . . . *L. collaris.*

Lysidice ninetta Audouin & Milne-Edwards, 1834

Lysidice ninetta, Augener, 1918, pp. 362–364.
Lysidice ninetta, Fauvel, 1923, pp. 411–412, fig. 162, *a–g.*

LOCALITIES. Off Accra: Stn. 48 (1), 13 mm. long, complete; Stn. 62 (1), 6 mm. long, anterior piece; from wood netted in 14 metres off Chorkor (1), 21 mm. long, complete.

For further details see below under *L. collaris.*

Lysidice collaris, Grube, 1869

Lysidice collaris, Crossland, 1903, pp. 143–144.
Lysidice collaris, Fauvel, 1932, pp. 143–144.
Lysidice collaris, Day, 1951, pp. 39–40.

LOCALITY. Off Accra, Stn. 62 (1), 22 mm. long, complete.

Differences, other than those noted in the above key, which serve to separate these two species are (*a*) a marked indentation on the anterior border of the prostomium compared with the almost entire border in *L. ninetta,* and (*b*) the greater development of the dorsal cirri in *L. ninetta.*

The form of the jaw articles do not differ sufficiently to warrant emphasis. Day (1951) has shown that this character is of value in differentiating between *L. collaris* and *L. natalensis,* particularly with respect to maxillae II. In *L. collaris* and *L.*

ninetta, however, the former has four teeth on each article of maxillae II, the latter varying between 4–4 and 4–5.

Chaetae are similar in both species. The simple types, capillaries and comb-like, are dorsal, the compound, with bidentate terminal articles, are ventral. In both species there are two pairs of anal cirri, a long dorsal pair and a short ventral pair.

DISTRIBUTION. *L. ninetta* is known extensively from, the European area in which *L. collaris* is unknown. There appears, however, to be a general overlap of the two species in the Pacific Panama, West African and Indian Ocean regions. *L. collaris* has been frequently recorded from the Indo-Pacific region, from Australia, China, Philippines, Japan, etc., in which areas no valid record of *L. ninetta* appears to have been made. The record of this latter species from New Zealand (Fyfe, 1952, p. 19) doubtfully accepted by Fauvel (1923, p. 411) and detailed by Augener (1924) as *L. brevicornis* Kinberg, is almost certainly *L. collaris*.

Subfamily ONUPHIDINAE

KEY TO GENERA

1. Branchial filaments inserted spirally . . . . *Diopatra*.
2. Branchial filaments simple or pectinate . . . . *Onuphis*.

Genus *DIOPATRA* Audouin & Milne-Edwards, 1833

Seven antennae, of which two are small frontals and five occipitals borne on ringed ceratophores. One pair of clear, translucent, circular areas posterior to the inner laterals, which are probably sensory in function. One pair of tentacular cirri on the apodous peristomium. Dorsal cirri subulate ; ventral cirri subulate in a few anterior segments thence becoming pad-like. Pseudo-compound chaetae in anterior segments, otherwise with simple capillary, comb-like and acicular chaetae. Branchiae large with filaments inserted spirally. Mandible of two pieces. Maxillae with a pair of forceps, three pairs of toothed plates and one unpaired plate. Tube parchment-like with agglutinated material of varying types.

KEY TO SPECIES

1. Tip of the shaft of the comb-chaetae continued as a central spike (Text-fig. 21, *a*). Tube as in Text-fig. 22, *a* . . . . *D. musseraënsis*.
2. Tip of the shaft of the comb-chaetae not so continued. Tube as in Text-fig. 22, *b*. *D. neapolitana*.

Diopatra musseraënsis Augener, 1918

Diopatra musseraënsis Augener, 1918, pp. 347–349, pl. 5, fig. 134 ; pl. 6, fig. 195 ; text-fig. 38, from Angola.

LOCALITIES. (1) Off Accra, dredge, 14·6 metres, in shingle 2 miles south from the mouth of the R. Densu (1), incomplete, 40 mm. long. (2) Winneba shore, 22.xi.49 (5), incomplete, 25–120 mm. long, with tubes measuring 160–240 mm. in length.

Strongly spiralled branchiae are present on about 50 chaetigers. The anterior dorsal surface is uniformly coloured mauve.

Chaetae are in well-defined groups. Prominent comb-chaetae (Text-fig. 21, *a*) are dorsal and anterior, they project almost as far as the stout winged capillaries which form a large group ventral to them. A bulbous parapodial cirrus projects beneath this latter group and divides the anterior set of pseudo-compound bristles from a small posterior group of capillaries. The pseudo-compound chaetae number four to a parapodium and have a darker brown terminal piece apparently grafted on to the light brown basal portion. This gives the effect of a possible articulating surface. Ventro-anteriorly to the ramal cirrus are two bidentate subacicular chaetae, which first appear at about the 17th parapodium.

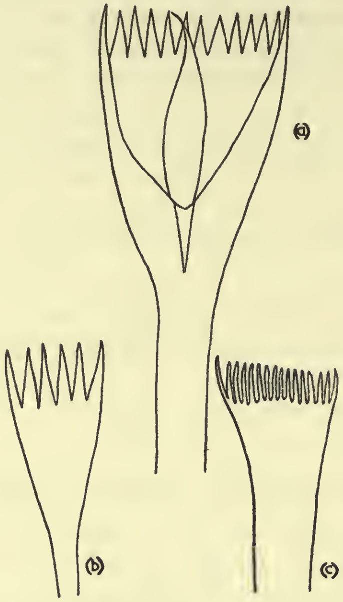

FIG. 21. Comb-chaetae of (*a*) *Diopatra musseraënsis*, × 500; (*b*) and (*c*) *Diopatra neapolitana*, × 750.

DISTRIBUTION. Known only from the above records.

Diopatra neapolitana Della Chiaje, 1841

Diopatra cuprea, Augener, 1918, pp. 350–354, text-fig. 39, from Elmina and Accra, Gold Coast, etc.
Diopatra neapolitana, Fauvel, 1923, pp. 419–420, fig. 166, *a–h*.
Diopatra neapolitana, Fauvel, 1933, pp. 28–37, figs. 3–4.

LOCALITIES. Off Accra: Stn. 6 (1), + tube; Stn. 16 (1); Stn. 27 (1), + tubes; Stn. 53 (1); Stn. 57 (34), + tubes; Stn. 58 (6), + tubes; Stn. 59 (1); Stn. 61 (1), + tubes; Stn. 70 (6); Stn. 73 (6), + tubes, one specimen complete, 30 mm. long; Stn. 110 (1), with tube; Stn. 111 (1), with tube; Stn. 126 (1), complete, 27 m. long. Apart from the specimens from Stns. 73 and 126, all are less than 15 mm. in length and are anterior fragments. Buchanan Survey, 3·6 to 11·0 metres off Accra (7), incomplete, up to 30 mm. in length.

In the complete specimen from Stn. 126 branchiae begin on the 5th parapodium and are spiralled up to the 30th foot, after which they become branched with one or two filaments for 10 segments and then disappear. The anterior dorsal surface is skin-coloured, crossed, in some specimens, by lateral stripes of pale mauve.

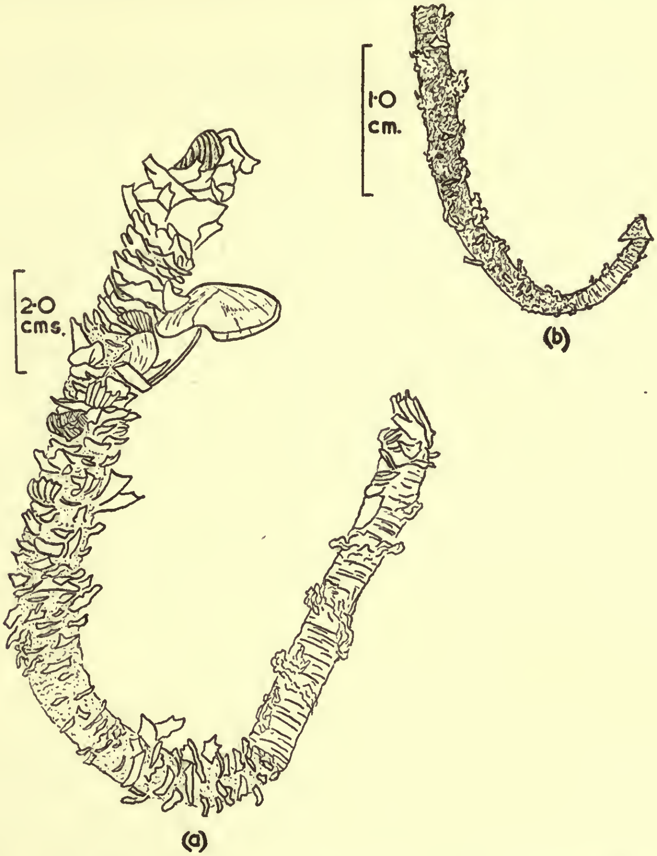

FIG. 22. Tubes of (*a*) *Diopatra musseraënsis*, (*b*) *Diopatra neapolitana.*

The form of the comb-chaetae in these specimens is illustrated in Text-figs. 21, *b–c*. These chaetae were exceedingly difficult to find and in no specimens were they as liberally distributed among the parapodia as in *D. musseraënsis*.

Fauvel (1932 & 1933) has drawn attention to the variation in form of the comb-chaetae in this species, and examination of the Gold Coast specimens supports his conclusions. In one specimen, for example, comb-chaetae with 6 and 14 teeth are present. For this reason Augener's record of 1918 of *D. cuprea* has been included as a synonym of *D. neapolitana*. With the exception of the scarcity of comb-chaetae in *D. neapolitana* the distribution of chaetae in the parapodia is very similar to that in *D. musseraënsis*.

DISTRIBUTION. Atlantic Ocean, Mediterranean Sea, Red Sea, Indian and Pacific Oceans.

Genus *ONUPHIS* Audouin & Milne-Edwards, 1833

Similar to *Diopatra* except that branchiae are not spirally coiled, but either simply branched or pectinate.

Onuphis eremita Audouin & Milne-Edwards, 1833

Onuphis landanaënsis, Augener, 1918, pp. 339–343, pl. 5, figs. 135–138, pl. 7, fig. 197, text-fig. 36.
Onuphis eremita, Fauvel, 1923, pp. 414–415, fig. 163, *a–l*.

LOCALITIES. (1) Tenpobo shore, about 30 specimens with tubes, some complete, measuring 30 mm. in length; associated with *Audouinia punctata*. (2) Off Accra: Stn. 57 (3), fragments, up to 18 mm. long; Stn. 12 (1), anterior piece.

Eyes are absent in this species. Branchiae begin on the first chaetiger with one filament; after 10 to 20 segments there is a gradual increase to a maximum development of five filaments. There are tri- or bidentate hooded pseudo-compound chaetae in the first three to five feet. Other chaetae are simple limbate capillaries and comb-like; acicular chaetae are bidentate. The specimens from Tenpobo are much smaller than those described by Fauvel. Tubes are of agglutinated sand grains with a few shell fragments.

DISTRIBUTION. Atlantic Ocean, Mediterranean Sea, Suez Canal, Madagascar, Ceylon, Madras, Mergui, Akyab, Caribbean Sea, and off the coast of South California down to Guatemala.

Subfamily LUMBRINERINAE

Genus *LUMBRINERIS* Blainville, 1828

Body long and cylindrical. Prostomium without palps, antennae or eyes. First two segments apodous and achaetous. Branchiae absent. Parapodia with two unequal ligules. Simple winged capillary chaetae and simple or compound hooks. Mandible bodice-like. Maxillae with four pairs of plates and two supports.

KEY TO SPECIES

1. Prostomium conical, pointed anteriorly; no compound hooded hooks, simple hooks as Text-fig. 23, *c* . . . . *L. impatiens*.
2. Prostomium rounded, blunt anteriorly with some compound hooded hooks (Text-fig. 23, *a*), simple hooks as in Text-fig. 23, *b* . . . . . . *L. albifrons*.

Lumbrineris impatiens (Claparède), 1868

Lumbriconereis impatiens, Fauvel, 1923, pp. 429–430, fig. 171, *a–i*.

LOCALITIES. (1) Tenpobo shore, 4.ii.50 (1), anterior piece 13 mm. long. (2) Accra, Christiansborg shore (2), one complete, 78 mm. long; one fragment, 20 mm. long.

Parapodia with a short, anterior, rounded lobe, and a long, posterior, cirriform ligule. Anterior parapodia have simple winged chaetae and simple hooks with denticles and guard. The capillaries are gradually replaced in the middle and posterior region, leaving only two or three simple hooks (Text-fig. 23, *c*) to each chaetiger. The large maxillary plates II have four teeth each, III 2 + 2 and IV 1 + 1. The maxillary supports are much longer than those described by Fauvel.

DISTRIBUTION. Atlantic Ocean, Mediterranean, Red Sea, Persian Gulf, Indian Ocean.

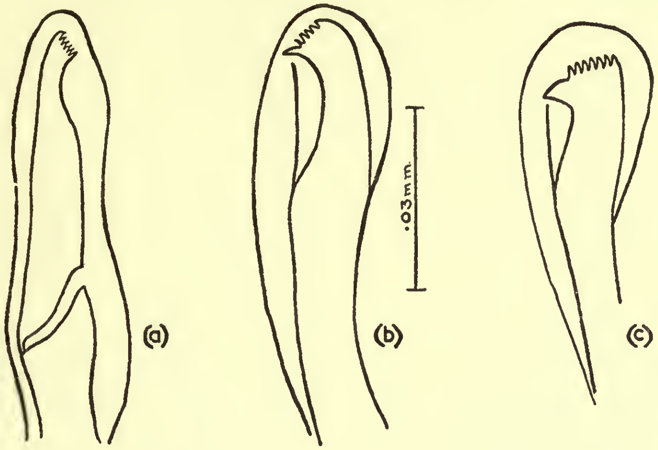

FIG. 23. Chaetae of *Lumbrineris*. (*a*) Compound hooded hook of *L. albifrons*, (*b*) simple hooded hook of *L. albifrons*, (*c*) simple hooded hook of *L. impatiens*.

Lumbrineris albifrons (Crossland), 1924

Lumbriconereis albifrons Crossland, 1924, pp. 50–55, text-figs. 65–72, from the Cape Verde Islands.

LOCALITY. Off Accra, from wood netted off Chorkor 24.v.51 (2), complete, 75 and 22 mm. long.

This species is characterized by the form of the compound chaetae (Text-fig. 23, *a*). These are, however, exceedingly difficult to find. The dental apparatus is illustrated in Text-fig. 24 and also serves to distinguish the species from closely related forms. Simple winged capillary chaetae are present with hooded hooks anteriorly, but are replaced by the latter posteriorly. As in *L. impatiens*, anterior parapodial lobes are short, posterior lobes are long.

DISTRIBUTION. The only authentic records of this species are those noted above; the records by Monro (1933) from the Galapagos Islands and Pruvot (1930) from, New Caledonia are of doubtful significance.

Subfamily LYSARETINAE

Apart from the characters noted above in the key, the following are of importance in this subfamily. Mandible of two pieces, maxillae with five pairs of symmetrical toothed plates and two long supports (Text-fig. 25).

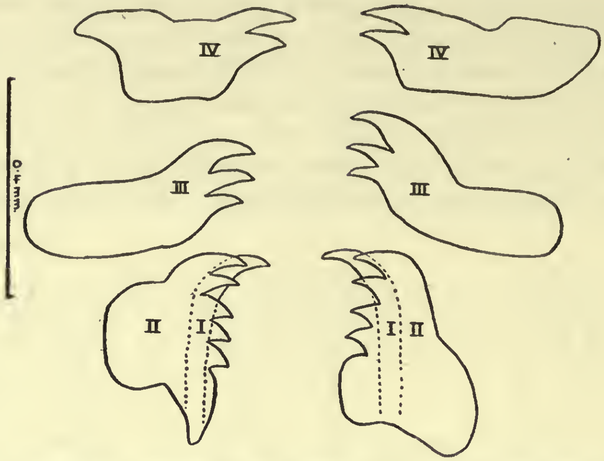

FIG. 24. *Lumbrineris albifrons.* Maxillae I to IV from the ventral surface.

Genus ***HALLA*** Costa, 1844

Prostomium oval with four eyes and three antennae on its posterior border. There are two anterior apodous and achaetous segments and no tentacular cirri. The dorsal cirri are large and foliaceous ; all chaetae are simple and acicular chaetae are present. Maxillae asymmetrical with two very long maxillary supports, (Text-fig. 25.)

Halla parthenopeia (Delle Chiaje), 1828

Halla parthenopeia, Fauvel, 1923, pp. 426–427, fig. 169, *a–h,* from Naples, Gênes and Cadiz.

LOCALITY. Off Accra, Buchanan Survey, in 3·6 to 11·0 metres depth (3), two anterior and one posterior pieces, between 85 and 110 mm. long.

Collector's note : " This worm is brick-red in life, blue in preservative. Grows up to 25 in. (625 mm.) long."

The specimens agree very well with Fauvel's description. The superior dorsal chaetae, however, are not as hispid as presented in his figure. Maxillary plates are illustrated in Text-fig. 25 and show the plates to have the following teeth : I 11–7, II 12–15, III 10–9, IV 11–11, V 1–1. There is, however, variation in this character and in the other specimens here examined the formulae is : I 11–8, II 12–13, III 16–12 +, IV 17–12, V 1–1. Many of the teeth are frequently broken, making accurate counting difficult. A dorsal incision was made in the pharynx in order to prepare Text-fig. 25, and the sets of teeth turned outwards. It appears, therefore, as if maxillae I and II of the right hand side worked against each other. In effect this maxillae I, with the basal portion of II, bites against I of the left hand side during mastication.

The large, foliaceous, dorsal cirri each bear an external notch basally, and the chaetae project laterally between the parapodial lobe and a secondary, anterior pedal flap.

Distribution. This appears to be the first record of this species in the Atlantic Ocean, south of Cadiz.

Family Orbiniidae

Body divided into two regions: (*a*) thorax, short and flat with few segments, neuropodia flattened pads with or without stout bristles; (*b*) abdomen, long and cylindrical, with numerous segments, neuropodia erect. Prostomium without ap-

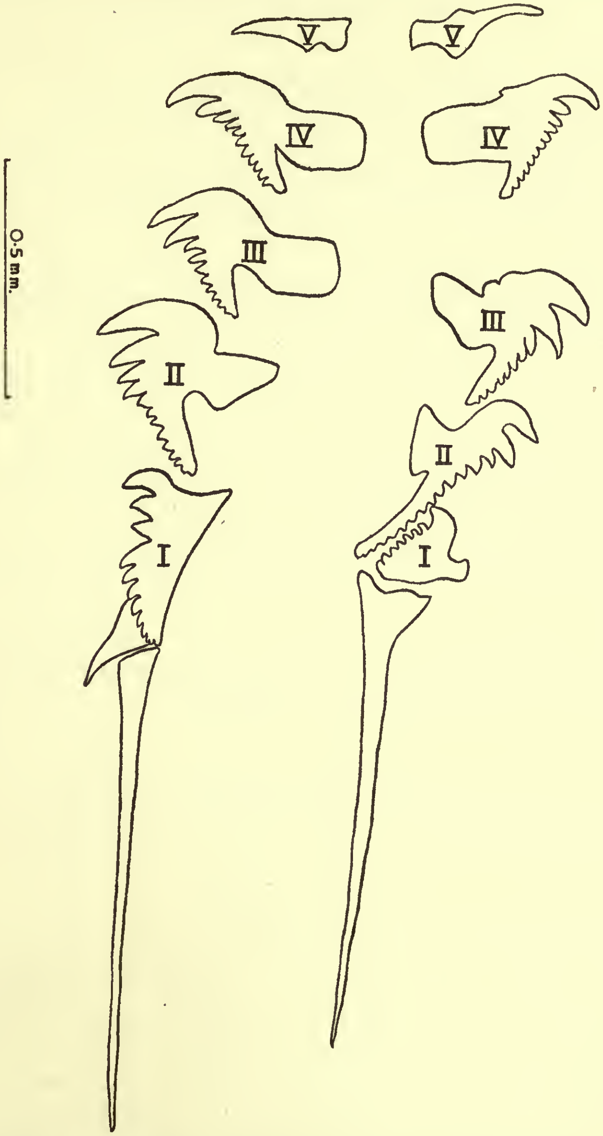

Fig. 25. *Halla parthenopeia*. Maxillae from the dorsal surface. (See text, p. 120, for explanation.)

pendages. Proboscis unarmed. Parapodia biramous with simple chaetae. Branchiae dorsal. Transverse rows of papillae often present on the ventral side of a number of thoracic segments.

KEY TO GENERA

1. Thoracic neuropodia with vertical rows of pedal papillae . . . . *Orbinia.*
   Thoracic neuropodia without vertical rows of papillae or with only 2–3 . . . . *2.*
2. Thoracic neuropodial chaetae entirely slender, pointed . . . . *Haploscoloplos.*[1]
   Thoracic neuropodial chaetae include pointed and hook-like ones . . . *Scoloplos.*

[1] Not recorded from the Gold Coast.

Genus *ORBINIA* Quatrefages, 1865

Prostomium conical. One pair of lanceolate gills on each segment except a few anterior ones. Thoracic notopodia with serrated capillary chaetae; neuropodia pad-like with stout chaetae and papillae. Abdominal notopodia with capillary and forked chaetae; neuropodia bilobed with capillary chaetae.

Orbinia foetida var. ***linguistica*** (Orlandi), 1896

Aricia foetida var. *linguistica*, Fauvel, 1927*a*, pp. 14–16, fig. 4, *a–l*.

LOCALITY. Off Accra, Buchanan Survey, in 3·6 to 11·0 metres (1), incomplete, 26 mm. long.

There are 22 segments in the thorax, branchiae begin on the 7th and ventral papillae appear on the 16th segment, with one pair and gradually increase to five pairs on segment 21; they are absent from segment 22. There are eight papillae on the posterior neuropodial lobe. Large lanceolate chaetae appear on the 11th to the last thoracic chaetiger. Between rami on abdominal segments there are pronounced cirri.

DISTRIBUTION. This variety appears to have been recorded only from the Mediterranean Sea, but the stem species is widely known from the English Channel and Atlantic Ocean and has been collected at Madagascar.

Genus *SCOLOPLOS* Blainville, 1820

Similar to *Orbinia*, but without pedal papillae or with only very few, 1–3, and never with inter-ramal cirri.

KEY TO SPECIES

1. With capillary chaetae in anterior thoracic neuropodia . . . . *2.*
   Without capillary chaetae in anterior thoracic neuropodia; with 23 thoracic segments, with branchiae beginning at the 6th; with 3 rows of hooks in thoracic neuropodia . . . . *S. johnstonei.*[1]
2. With pedal papillae on anterior thoracic neuropodia; with 12 to 20 thoracic segments, with branchiae beginning at the 9th to 17th. . . . . *S. armiger.*[1]
   Without pedal papillae on anterior thoracic neuropodia . . . . . . *3.*
3. Branchiae begin on anterior thoracic segments . . . . . . *S. dubia* sp. n.
   Branchiae begin on posterior thoracic or anterior abdominal segments *S. madagascarensis.*

[1] Not recorded from the Gold Coast.

Scoloplos madagascarensis Fauvel, 1919

Scoloplos madagascarensis Fauvel, 1919, pp. 433–434, pl. 17, figs. 81–86.

LOCALITY. Off Accra, Buchanan Survey, in 3·6 to 11·0 metres (2), anterior pieces, each 33 mm. long ; there are also two median pieces which may be detached portions of the anterior parts.

In one of the anterior pieces the thorax is made up of 21 segments, of which the first nine have two rows of neuropodial hooks and the remainder one. Branchiae appear on the last thoracic segment, on which there is also one pedal papilla. In the other anterior piece there are 26 thoracic segments, all of which have one row of neuropodial hooks. Branchiae appear on the first abdominal segment. This piece is without pedal papillae.

Both specimens have a few short forked chaetae in abdominal notopodia, one arm of the fork being about twice as long as the other. These chaetae are very easily broken and difficult to find.

Fauvel (1919) originally described *S. madagascarensis* with a thorax of 26–27 segments and with branchiae appearing at the 21st or 22nd segments becoming fully developed at the 25th or 26th. It will be seen that the specimens from Accra agree in one or other of these characters, and it is suggested that the species may be more variable than has hitherto been indicated.

DISTRIBUTION. Previously recorded from Madagascar and Inhaca Island, Delgoa Bay, Transvaal (Day, 1951).

Scoloplos dubia sp. n.

Holotype ; B.M. (N.H.) Reg. No. 1953.3.1.1230.

LOCALITY. Off Accra, Buchanan Survey, in 3·6 to 11·0 metres depth, complete, about 90 mm. long.

The sharply pointed prostomium is without visible eyes. There are 22 thoracic segments. Thoracic neuropodial capillaries (Text-fig. 26, *a*) appear on every foot ; notopodial chaetae throughout the body are similar to these. Forked notopodial chaetae have not been seen. Thoracic neuropodial hooks are shown in Text-fig. 26, *b*, they occur in three to four rows on each segment. In the posterior region of the abdomen the neuropodial aciculae become external and hooked (Text-fig. 26, *c*).

Paratypes ; B.M. (N.H.) Reg. No. 1953.3.1.1231–4, from the same locality as the holotype.

These specimens are all incomplete, the longest measuring 65 mm. In all of them the branchiae appear at the 7th foot ; in two the thorax has 22 segments, in one 21 and in the other 23. In other characters they are identical with the holotype.

As suggested by its name the status of this new species is doubtful. It is undoubtedly closely related to *S. johnstonei*, from which it is distinguished principally in having thoracic neuropodial capillaries and posterior hooked aciculae. Examination of material from areas between the Gold Coast and the Cape of Good Hope (the distributional zone of *S. johnstonei*) may clarify the relationship.

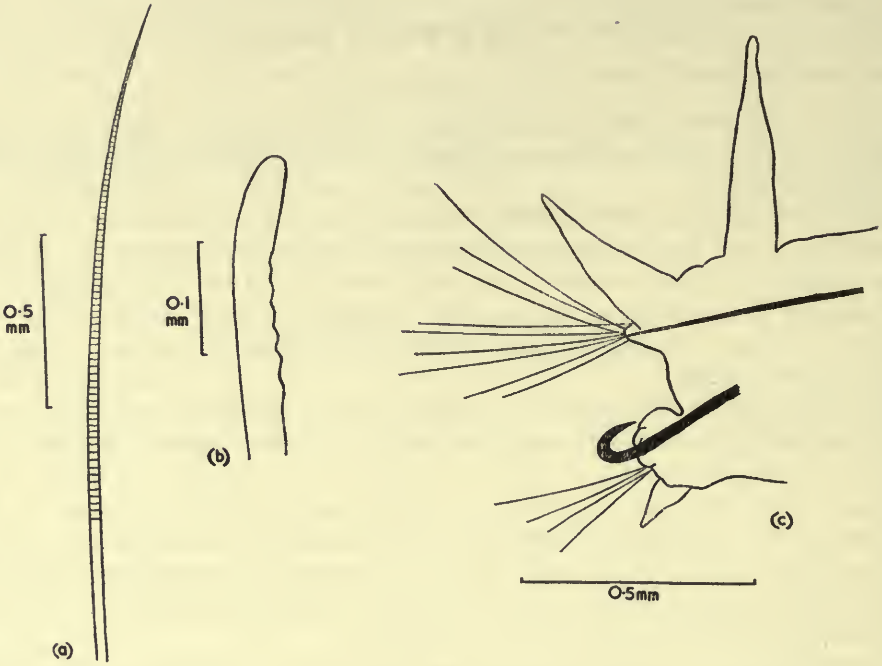

FIG. 26. *Scoloplos dubia* sp. n. (*a*) Thoracic neuropodial chaeta, (*b*) thoracic neuropodial hook, (*c*) posterior abdominal parapodium.

Family SPIONIDAE

Body not divided into distinct regions. Prostomium without antennae; (sometimes with frontal peaks); with palps and eyes. Biramous parapodia with foliaceous ventral and dorsal cirri; dorsal branchiae on a number of segments. Chaetae simple capillaries and hooded hooks.

Genus ***PRIONOSPIO*** Malmgren, 1867

Prostomium without frontal peaks. Branchiae 3–11 pairs, often pinnate, confined to anterior segments. Simple capillaries and pluridentate hooded hooks are present.

Prionospio pinnata Ehlers, 1901

Prionospio africana, Augener, 1918, pp. 402–5, pl. 6, figs. 162–3, text-fig. 51.
Prionospio pinnata, Fauvel, 1932, p. 173.

LOCALITIES. Off Accra, Stn. 69 (2), incomplete, both 7 mm. in length; Buchanan Survey, off Accra, 3·6 to 11·0 metres, depth (7), one complete, 55 mm. long, others incomplete 10–41 mm. long.

Pinnate branchiae, if present, occur on the first three chaetigers only, frequently they have been accidentally lost. Several of the specimens from the Buchanan

Survey still retain one of the long pair of palps, which extends from the posterior region of the prostomium to the 16th chaetiger. The palps are somewhat curved and grooved dorsally (Text-fig. 27). Their external margin is marked with mauve vertical stripes. Four eyes are set in a trapezium on the prostomium, which is enclosed between two membranous wings. Within these wings the prostomium consists of a prominent longitudinal ridge.

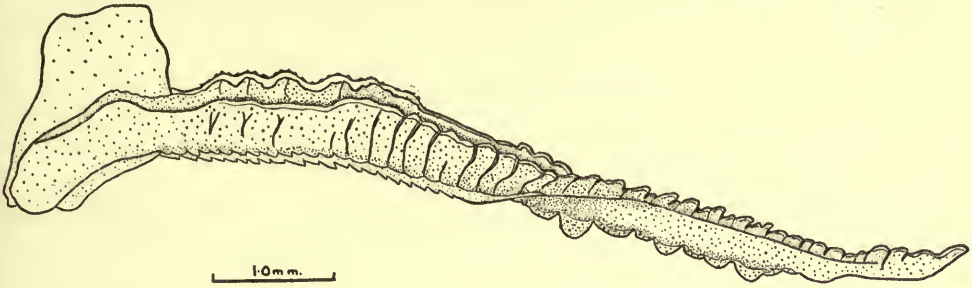

Fig. 27. *Prionospio pinnata.* Grooved palp from the left hand side of the prostomium. (Specimen from the Buchanan Survey.)

Distribution. Atlantic Ocean, Indian Ocean and Pacific Ocean.

Family CIRRATULIDAE

Body short, cylindrical, with numerous segments ; head without appendages, with or without eyes. Proboscis smooth, unarmed. Dorsal palps or tentacular cirri on an anterior segment ; long slender branchiae inserted above the notopodia ; parapodia biramous ; chaetae simple capillaries and acicular hooks.

Key to Genera

1. Branchiae appearing on the same segment as the tentacular cirri . . . *Cirratulus.*
2. Branchiae appearing on a few segments in front of the one bearing tentacular cirri *Audouinia.*

Genus *AUDOUINIA* Quatrefages, 1865

First three segments achaetous. Branchiae occur on the first chaetigers to nearly the last ones. Of the three species of this genus recorded here, each is confined to a particular area of the Gold Coast. Thus *A. punctata* has been found only in the Tenpobo area ; *A. tentaculata* only on the Winneba shore, and *A. filigera* only in the Sekondi-Axim region. No overlap has been noted.

Key to Species

1. Branchiae in the middle body region situated half the distance above the notopodium that the notopodium is above the neuropodium . . . . *A. tentaculata.*
   Branchiae in the middle body region situated much more than half the distance above the notopodium than the notopodium is above the neuropodium . . 2.

2. One hook in the neuropodium in the posterior part of the body. Branchiae in the middle body region situated, normally, much further than twice as far above the notopodium as the notopodium is above the neuropodium . . . . *A. filigera.*
Three or more hooks in the neuropodium in the posterior part of the body. Branchiae in the middle body region situated at least as far above the notopodium as the notopodium is above the neuropodium . . . *A. punctata.*

Audouinia tentaculata (Montagu), 1808

Cirratulus tentaculatus var. *meridionalis*, Augener, 1918, pp. 461–463, pl. 6, fig. 175—176.
Audouinia tentaculata, Fauvel, 1927*a*, pp. 91–92, fig. 32, *a–g*.

Locality. Winneba shore, 22.xi.49 (20), between 18–35 mm. long, and another ten specimens, badly mutilated, in association with tubes of *Sabellaria eupomatoides* from this area collected on the same day.

The tentacular cirri appear between the 6th and 7th chaetigers. Typically there are two hooks in the neuropodia over the greater part of the body, though for some segments after the 12th foot there may be three to four.

Distribution. Common in the European zone from the North Sea, Irish Sea, English Channel and the Atlantic Ocean. Known also from German South-West Africa (Augener, 1918) and the Cape (Day, 1951).

Audouinia filigera (Delle Chiaje), 1841

Audouinia filigera, Fauvel, 1927*a*, pp. 92–93, fig. 32, *h–m*.
Audouinia filigera, Fauvel, 1932, p. 178.

Localities. (1) Sekondi, high level plateau, 21.ii.49 (4), complete, up to 20 mm. long. (2) Dixcove, shore (12), mutilated, 20–40 mm. long. (3) Princes Town, shore, 15.iv.49 (4), complete, 20–25 mm. long. (4) Axim, Hospital Reef (3), 10–12 mm. long.

The tentacular cirri occur between the 4th and 5th chaetigers. After the appearance of two neuropodial hooks at the 12th foot, which persist for a small number of segments, there is a reduction to one, which condition is maintained up to the end of the body.

Distribution. Well known from the Atlantic Ocean, Persian Gulf, and the Indian and Pacific Oceans.

Audouinia punctata (Grube), 1858

Cirratulus punctatus, Augener, 1918, pp. 465–467.
Audouinia punctata, Day, 1951, p. 47.

Locality. Tenpobo shore, approximately 370 specimens, measuring up to 20 mm. long were collected here during February, 1950.

The tentacular cirri are situated between the 3rd and 4th chaetigers. There are normally three hooks in the neuropodium over the greater part of the body, but anteriorly (i.e. just after the 12th parapodia) there may be a reduction to two and posteriorly an increase to four. Colour in spirit grey-black, flecked with black, but considerable areas of white may be present ; white to grey tentacular cirri with black lateral stripes; gills grey black with sometimes an orange tip; young forms brown.

DISTRIBUTION. This species is known from the Atlantic, south of Florida to the Cape of Good Hope, and from the Natal coast.

Genus ***CIRRATULUS*** Lamarck, 1818

Similar to *Audouinia* except as in above Key.

Cirratulus filiformis Keferstein, 1862

Cirratulus filiformis Fauvel 1927*a*, pp. 94–95, fig. 33, *h*.

LOCALITY. Off Accra, Buchanan Survey, in 3·6 to 11·0 metres (5), all incomplete, the largest piece measuring 38·0 mm. long.

The prostomium is sharply pointed, and has no eyes. On the 1st chaetiger there is one pair of long and filiform branchiae and these are present up to the end of the body. All chaetae are simple capillaries, there are no hooks present. Anteriorly segments are narrow; posteriorly they are long.

DISTRIBUTION. This species is well known from West European waters and has been reported from Senegal by Fauvel (1902).

Family FLABELLIGERIDAE

Prostomium and peristomium with eyes, palps and branchiae, completely retracted into the oral aperture, made visible only by dissection. Chaetae of anterior segments long, directed forwards to form a cephalic cage. Parapodia biramous and normally without distinct processes. Notopodial chaetae simple; neuropodial chaetae sigmoid or hooked or compound with a sickle-shaped terminal piece.

Genus ***STYLARIOIDES*** Delle Chiaje, 1828

Body elongated, with numerous papillae on its surface. Prostomium with two stout palps. Branchiae filiform, on a peduncle, retractile. Notopodial chaetae simple capillaries, annulated; neuropodia with simple capillaries and sometimes with strong hooks.

KEY TO SPECIES

1.	Neuropodial chaetae long and slender throughout	*S. scutigeroides.*
	Some neuropodial chaetae hooks	*2.*
2.	Neuropodial hooks with bidentate tips	*S. arenosus.*
	Neuropodial hooks with entire tips	*S. tropicus.*

Stylarioides scutigeroides Augener, 1918

Stylarioides scutigeroides Augener, 1918, pp. 444–447, pl. 6, figs. 155 and 185, text-fig. 66.

LOCALITIES. Off Accra: Stn. 55 (1); Stn. 69 (4); Buchanan Survey, in 3·6 to 11·0 metres (5), only four of these specimens are complete, measuring between 15 and 30 mm. in length.

The complete body consists of 70 parapodia. The 1st chaetiger is telescoped into the 2nd, the 2nd into the 3rd and the 3rd into the 4th. Thereafter the segments are separated only by intersegmental grooves anteriorly and ridges posteriorly.

Chaetae of the first parapodia vary between 2·5 to 4·5 mm. in length (Text-fig. 28, *a* and *b*) and are directed forward, forming the characteristic cephalic cage of the Flabelligeridae. Chaetae of the second parapodia are between 1 and 2·5 mm. long and are also directed anteriorly. Thereafter the chaetae decrease in size and project laterally. Notopodia and neuropodia in the first and second parapodia are close together, elsewhere they are far apart. The anterior region of the body is swollen, posteriorly it narrows, so that in one specimen the width across the 12th segment is 2·5 mm. and across the 30th, 0·5 mm. Except for a few posterior segments the body is heavily encrusted with sand grains.

All chaetae are long and slender ; notopodial bristles are illustrated in Text-fig. 28, *d*, neuropodial bristles in Text-fig. 28, *c*. Papillae are present all over the body but are hidden to superficial view by the heavy encrustation of sand. On the first and second parapodia a single finger-shaped papilla, which may be bi- or trifid terminally, is associated with each group of chaetae, and there are sometimes one or two interramal in position. On the 3rd and 4th chaetigers simple finger-shaped papillae are present between the rami, encircling the segments like coronets. There are 6–7 dorsally between the notopodia, 2–3 laterally between the notopodia and neuropodia and 6–7 ventrally between the neuropodia. After the 5th segment the papillae become smaller and more scattered in arrangement. Posteriorly they are less numerous.

DISTRIBUTION. *S. scutigeroides* is known only from the Gold Coast, the French Congo and Cabinda.

Stylarioides arenosus (Kinberg), 1867

Pycnoderma fernandense, Augener, 1918, pp. 448–452, pl. 6, figs. 148, 182 ; pl. 7, figs. 237, 238 ; text-fig. 67, from Saltpond, Gold Coast.

This species has not been collected in the present survey. Stout neuropodial chaetae, with bidentate tips appear at the 5th chaetiger. The secondary tooth at the tip is easily broken and the chaetae have frequently been described as unidentate. Papillae run along the body in longitudinal rows between the rami. Normally there are between 10 to 12 to each segment, four ventral and four dorsal and one or two laterally. One of Augener's largest specimens measured 39 mm. long for 75 segments, but Hartman (1948) found one of Kinberg's types measured 60 mm. for 70 segments.

DISTRIBUTION. Around the coast of Africa from the Gold Coast to Natal.

Stylarioides tropicus Augener, 1918

Stylarioides tropicus Augener, 1918, pp. 437–440, pl. 7, figs. 220, 221, text-fig. 63.

This species has not been collected in the present survey. It appears to be characterized by strong hooks with entire tips which appear at the 4th chaetiger, otherwise Augener's description is difficult to follow. One of Augener's specimens measured 24 mm. long for 32 segments.

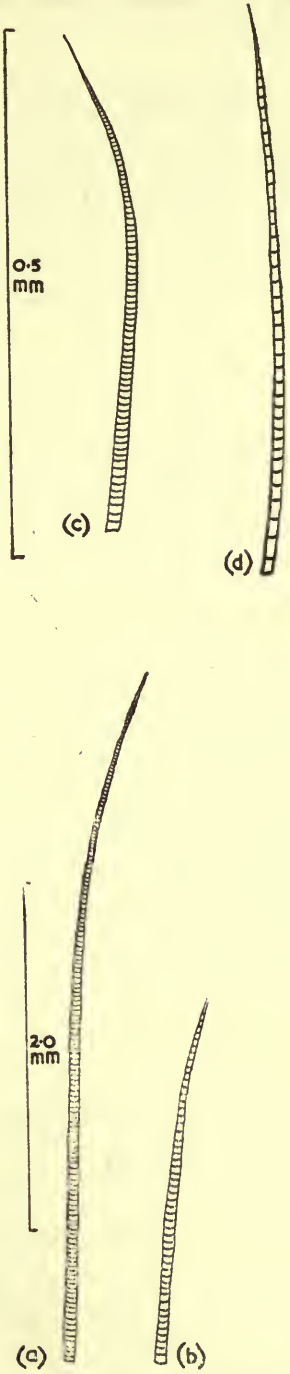

FIG. 28. *Stylariodes scutigeroides.* Chaetae ; (*a*) and (*b*) of the cephalic cage ; (*c*) neuropodial ; (*d*) notopodial.

DISTRIBUTION. The species was collected from Liberia, the Gold Coast, Accra, French Congo, Cabinda and Angola.

Family OPHELIIDAE

Body short, convex dorsally, with or without a gutter ventrally. Prostomium without appendages, frequently with cephalic eyes. Sometimes with lateral eye spots. Biramous parapodia with simple chaetae. Pygidium with papillae or sometimes prolonged into an anal tube.

KEY TO GENERA

1. With lateral branchiae . . . . *Armandia.*
2. Without lateral branchiae . . . . *Polyophthalmus.*

Genus ***ARMANDIA*** Filippi, 1861

Body not divided into distinct regions; a deep median and two lateral ventral grooves. Branchiae from the 2nd chaetiger to the end of the body. Pygidium with anal funnel fringed with papillae and a median cirrus. Lateral eye-spots.

Armandia intermedia Fauvel, 1902

Armandia intermedia Fauvel, 1902, pp. 86–89, figs. 29, 30, from Senegal.
Armandia intermedia, Augener, 1918, pp. 424–425, from Senegal and Angola.
Armandia intermedia, Day, 1949, p. 449, from St. Helena.

LOCALITY. Off Accra, Stn. 69 (1), 12 mm. long.

There are 29 chaetigers, the 1st abranchiate, the next 25 branchiate (though some of the posterior branchiae have fallen off, the point of attachment to the superior edge of the parapodia can be seen), and the last three abranchiate. Thirteen pairs of lateral eye-spots are situated on the 7th to the 19th chaetigers. There are three cephalic, subcutaneous, eye-spots disposed in a triangle. The anal funnel is fringed with numerous papillae, but many have fallen off and the exact number cannot be estimated.

DISTRIBUTION. This species is only known through the above records.

Genus ***POLYOPHTHALMUS*** Quatrefages, 1850

Similar to *Armandia* but with no branchiae.

Polyophthalmus pictus (Dujardin) 1839

Polyophthalmus pictus, Fauvel, 1927*a*, pp. 137–138, fig. 48, *l–o*.

LOCALITIES. (1) Tenpobo shore, 6.ii.50 (2), 6–8 mm. long; (2), Lighthouse Reef, Axim, 8.i.51 (1), 9 mm. long.

There are 28 chaetigers with about 11 pairs of eye spots on the 6th to 16th segments, but these are very difficult to see and may vary considerably in position.

DISTRIBUTION. English Channel, Atlantic, Mediterranean, and the Red Sea; Pacific and Indian Oceans.

Family MALDANIDAE

Body of few segments some of which are exceptionally long. Prostomium without appendages, often with a rimmed cephalic plate and a median keel, on each side of which is a nuchal groove. Buccal segment achaetous. Parapodia biramous, notopodial chaetae capillaries, neuropodial chaetae uncinate; no parapodial cirri. Anal segment with funnel and cirri or a flat plate. Inhabitants of cylindrical tubes which may be thin and covered with sand or thick and coated with mud.

Genus ***MALDANE*** Grube, 1860

Cephalic keel arched, rim divided into three by two lateral notches. Anus dorsal with a slanting anal plate. Ante-anal segments achaetous. Neuropodial chaetae missing from the first segment. Notopodial chaetae of three kinds. Tube coated with mud.

Maldane sarsi Malmgren, 1865

Maldane sarsi, Fauvel, 1927*a*, pp. 197–199, fig. 69.

LOCALITY. Off Accra, Buchanan Survey, in 36·5 metres off Castle (1), complete, about 62 mm. long.

Prostomium with the cephalic keel strongly arched and the rim smooth, but notched on each side.

The nuchal grooves are short, curved and deep. There are 19 chaetigers and two achaetous ante-anal segments. Notopodial chaetae are of three types: (*a*) long capillaries, barbed along their entire length; (*b*) limbate capillaries, slightly barbed at their tips; (*c*) very short geniculate capillaries with a limb on their convex borders.

Uncini with one very large tooth surmounted by 5–6 rows of smaller teeth; beneath the large tooth there is a cluster of fine hairs.

DISTRIBUTION. Cosmopolitan.

Family OWENIIDAE

Cylindrical body of few segments having the prostomium fused with the buccal segment and being either devoid of appendages or terminating in a membranous lobe. Notopodial chaetae simple capillaries; neuropodial chaetae uncinate, very small, with a bent hooked tip. Tube coated with sand and shell fragments.

Genus ***OWENIA*** Delle Chiaje, 1841

Prostomium terminating in a membranous branchial lobe. Buccal segment achaetous; the first three chaetigers without uncini. Notopodial chaetae slender, slightly spinous. Pygidium bilobed.

Owenia fusiformis Delle Chiaje, 1841

Owenia fusiformis, Fauvel, 1927*a*, pp. 203–204, fig. 71, *a–f*.
Owenia fusiformis, Augener, 1918, pp. 492–493.

LOCALITIES. Off Accra: (*a*) Stn. 5 (25); Stn. 11 (4); Stn. 32 (numerous); Stn. 53 (24); Stn. 54 (numerous); Stn. 55 (50 +); Stn. 61 (7); Stn. 65 (numerous); Stn. 66 (numerous); Stn. 67 (36); Stn. 121 (2); Buchanan Survey, 3·6 to 11·0 metres (9); (*b*) Dredge haul off Chorkor, 1.xi.50 (20).

The animals vary in length between 40–60 mm., the tubes, many of which are empty, particularly from Stns. 55, 65 and 66, measure up to 88 mm. The thorax consists of the achaetous buccal segment and the first three chaetigers which have only notopodial capillaries; there is no neuropodial component in this region. The remaining segments, which are all biramous, make up the abdomen, and are long in the anterior region, but posteriorly become progressively smaller. The tubes consist of agglutinated small shells and sand, the former orientated at right angles to the long axis, and are grey in colour.

DISTRIBUTION. Cosmopolitan.

Family SABELLARIIDAE

Body divided into four regions, (*a*) an anterior region with opercular disc and stalk, (*b*) a thorax of two anterior and three or four parathoracic segments, (*c*) an abdomen with uncinigerous dorsal rami and ventral rami with capillaries, (*d*) a caudal region, unsegmented, achaetous and apodous. The prostomium is hidden between the two large opercular stalks which carry paleae in concentric rows. Two palps. Simple branchiae are carried on the thorax and abdomen. Tubes are laid down and normally form sandy reefs of varying extent; occasionally species may be solitary.

Genus ***SABELLARIA*** Lamarck, 1818

The operculum is short, with numerous filiform tentacles on the ventral side and provided with three visible rows of paleae. (The middle and inner rows probably represent a single row.) Thorax with two anterior segments, having only capillary chaetae, and three parathoracic segments with flattened paleae dorsally and similar, smaller chaetae, ventrally.

KEY TO SPECIES

1. Animal small, less than 10 mm. in length when sexually mature; tubes made up of small particles of sand . . . . *S. eupomatoides*.
   Animals large, more than 15 mm. in length when sexually mature; tubes made up of large and coarse sand grains . . . . 2.
2. Central tooth of outer paleae bluntly spatulate, entire or bifid *S. spinulosa* var. *intoshi*.
   Central tooth of outer paleae with a barbed point . . *S. spinulosa* var. *alcocki*.

Sabellaria eupomatoides Augener, 1918

Sabellaria eupomatoides Augener, 1918, pp. 503–504, pl. 7, figs. 187–190, text-fig. 83, from Angola.

LOCALITIES. Numerous masses of the tubes of this species were collected from Winneba shore, Apam shore and Christiansborg shore at various times in 1949; specimens normally measure between 5–8 mm. in length.

This species is characterized by its small size (a mature female from Winneba, collected 22.xi.49, measured 7 mm. long) and the form of the opercular paleae (Text-fig. 29). In some specimens several paleae of the median row project above the level of the others. There are nine pairs of simple gills from the 2nd thoracic segment backwards.

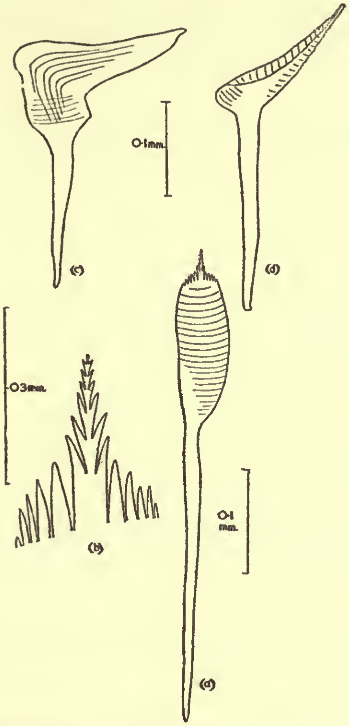

FIG. 29. *Sabellaria eupomatoides*. Opercular paleae: (*a*) from the external row; (*b*) enlarged terminal piece of (*a*), (*c*) from the outer row and (*d*) from the median row. (Specimen from Winneba.)

S. eupomantoides was described by Augener in 1918 from specimens collected without their tubes, and has not been recorded since then except as above.

Sabellaria spinulosa Leuckart, 1849

Acicular chaetae are present on the dorsal face of the operculum, immediately posterior to the terminal crown of paleae. There is an inter-peduncular cirrus. Paleae in the external row have a barbed median tooth.

Sabellaria spinulosa var ***intoshi*** Fauvel, 1914

Sabellaria spinulosa var. *intoshi* Fauvel, 1927*a*, pp. 208–211, fig. 73*p*.

LOCALITIES. (1) Tenpobo shore, about 20 specimens and tubes were collected in January and February, 1949, several were complete and measured up to 36 mm. long without the tail. (2) Apam (1), incomplete, 20 mm. long, and numerous tubes. (3) Dixcove shore (1), incomplete, 30 mm. long, with tube. (4) Axim Lighthouse Reef, 14.iv.49 (4), up to 38 mm. long, with tubes.

This variety differs from the stem species in having the median tooth of paleae of the outer row with a spatulate tip. Occasionally this tip may be bifid.

DISTRIBUTION. English Channel and the Atlantic ocean (Gulf of Guinea).

Sabellaria spinulosa var ***alcocki*** Gravier, 1906

Sabellaria spinulosa var *alcocki*, Fauvel, 1927*a*, pp. 208–211, fig. 73, *k–m*.

LOCALITY : Axim, Hospital Reef, 7.i.51 (1), 18 mm. long, with tube.

Some of the paleae in the median row are always erect in this variety, otherwise it is similar to the stem species.

DISTRIBUTION. English Channel, North Sea, Atlantic Ocean, Indian Ocean and the Red Sea.

Family STERNASPIDAE

The form adopted in the family is aberrant. The body is swollen at both ends; the prostomium small and devoid of appendages; the first three segments have chaetae, the middle ones are achaetous, and posteriorly there is a ventral shield from the borders of which chaetae radiate. Branchiae are posterior to the shield.

Genus ***STERNASPIS*** Otto, 1820

Branchiae filiform, set in two bundles.

Sternaspis scutata (Ranzani) var. ***africana*** Augener, 1918

Sternaspis fossor Stimpson var. *africana* Augener, 1918, pp. 608–613, text-fig. 109.
Sternaspis scutata var. *africana*, Monro, 1930, pp. 179–180.

LOCALITIES. Off Accra: Stn. 27 (42); Stn. 28 (2); Stn. 33 (6); Stn. 47 (2); Stn. 59 (1); Stn. 61 (8); Stn. 68 (14); Stn. 69 (19); Stn. 71 (3); Stn. 130 (1); Buchanan Survey, 3·6 to 11·0 metres (4).

The specimens vary between 5 and 15 mm. in length, but these measurements must be treated with caution, for in many cases the anterior chaetigers have contracted into the succeeding segments.

As Augener (1918) and Monro (1930) pointed out, the variety is distinguished. from the stem species by the greater number of chaetae (about 20 as opposed to 10–12) which occur on the anterior segments. The chaetae are also more slender in the variety. These small differences seem to divide clearly the West African forms from the European and Antarctic examples, though further examination may indicate that the difference is merely ecological. Thus *S. scutata* has been reported from 68–1080 metres (Monro, 1930), from about 300 metres (Chamberlin, 1919), and *S. fossor* from 68–130 metres, (Fauvel, 1936) and from 120–130 metres, (Takahasi, 1938), whereas *S. scutata* var. *africana* has not been reported beyond a depth of 67 metres. Unfortunately many scattered records of the parent species do not give depth details or particulars of the morphological differences noted above, so that an accurate consideration of this issue is not possible. However, further collecting, at depth, off the Gold Coast may clarify the matter, and if it is confirmed that the morphological differences are non-genetic, but induced by the ecological conditions, the taxonomic treatment must be modified. If they prove to be genetic and associated with geography *africana* must rank as a subspecies.

DISTRIBUTION. *S. scutata* var. *africana* is only known from off the W. African coast, from Senegal south to Angola.

Family AMPHARETIDAE

Body divided into two regions, (a) thorax with notopodial capillaries and neuropodial uncini, (b) abdomen with neuropodial uncini only. Tentacles retractile into the mouth. There are three or four pairs of branchiae on anterior segments and they may be subulate, pectinate or bi-pectinate. With or without groups of paleae.

KEY TO GENERA

1. With paleae and without dorsal hooks behind the branchiae . . . . . . 2.
   Without paleae and with dorsal hooks behind the branchiae . . . . *Isolda.*
2. With one of the four pairs of branchiae pectinate ; 17 thoracic chaetigers *Phyllamphicteis.*
   With one of the four pairs of branchiae bi-pectinate ; 16 thoracic chaetigers *Pterolysippe.*

Genus *PHYLLAMPHICTEIS* Augener, 1918

With two fan-like groups of paleae ; thorax of 17 chaetigers with uncini appearing at the 4th. Abdomen of 15 chaetigers. Four pairs of branchiae, three subulate, one pectinate.

Phyllamphicteis collaribranchis Augener, 1918

Phyllamphicteis collaribranchis Augener, 1918, pp. 509–512, pl. 7, figs. 239–241, text-fig. 85, from Wappu on the Ivory Coast.

LOCALITIES. Off Accra : Stn. 28 (1) ; Stn. 33 (1) ; Stn. 69 (1) ; Stn. 70 (1) ; Stn. 97 (4) ; Stn. 111 (1) ; several of these specimens are complete measuring up to 20 mm. long.

There are 8–10 paleae in each fan. Thoracic uncini have five teeth ; notopodial capillaries are slightly limbate. Both parapodial rami have small cirri on thorax and abdomen. The tubes are of fine dark grey mud with a few adhering shell particles.

Four specimens collected in the Buchanan Survey, in 3·6 to 11·0 metres off Accra and measuring between 20 and 30 mm. long, differ from the above in having two pairs of pectinate branchiae instead of one, though similar in other respects. It may be that they represent a different species, but it is possible that there is a considerable range of variation in this character within the species. Additional material and observations are needed to settle this point.

DISTRIBUTION. Only known from the above records.

Genus ***PTEROLYSIPPE*** Augener, 1918

With two groups of paleae, each like a fan. Thorax of 16 chaetigers with uncini appearing at the 4th. Four pairs of branchiae, 3 subulate and the other bi-pectinate.

Pterolysippe bipennata Augener, 1918

Pterolysippe bipennata Augener, 1918, pp. 512–514, plate 6, figs. 173 & 174, text fig. 86, from Whydah, Dahomey.

LOCALITIES. Off Accra: Stn. 59 (1), with tubes; Stn. 133 (1); Buchanan Survey, in 3·6 to 11·0 metres (4), and in 41·86 metres off the Lagoon (1); several of these specimens are complete and measure up to 18 mm. long.

The prominent bi-pectinate gill is coloured with numerous small purple marks. There are 15 abdominal segments. Thoracic uncini have 5–6 teeth, notopodial chaetae are limbate. Branchiae become easily detached in this species and it is rare to find a specimen with the complete set. No cirri are visible on the parapodia. Tubes are thick, of fine grey-black mud.

DISTRIBUTION. Only known through the above records.

Genus ***ISOLDA*** Muller, 1858

Without paleae. Number of thoracic and abdominal segments variable. Four pairs of branchiae, two subulate, and two feather-like. Two dorsal anterior hooks, immediately behind the branchiae.

Isolda whydahensis Augener, 1918.

Isolda whydahensis Augener, 1918, pp. 514–518, pl. 7, fig. 216, text-fig. 87.

LOCALITY. Off Accra, Buchanan Survey, in 5·5 metres off the breakwater (1), incomplete, length 15 mm.

There are 16 thoracic chaetigers the first three of which are very difficult to see. They lie on the prostomial collar and in the specimen examined the chaetae had been broken off. Neuropodial uncini appear at the 5th chaetiger, are short and have five teeth. Thoracic capillaries are limbate. The transverse membrane which, with the prostomial collar, encloses the branchiae and dorsal hooks, is smooth. Both of the inner pairs of branchiae are feather-like, the outer pairs are subulate.

DISTRIBUTION. *I. whydahensis* is known also from Whydah, Dahomey, the French Congo and Angola.

Family TEREBELLIDAE

Body with thorax having notopodial capillary chaetae on all chaetigers and neuropodial uncini on some, and abdomen with neuropodial uncini only. Prostomium with non-retractile tentacles. Branchiae, when present, normally on the anterior segments. In the thorax there are ventral glandular scutes. The tubes are coated with sand.

KEY TO GENERA

1.	Without branchiae	*Amaea.*
	With branchiae	2.
2.	With a single quadripartite pectinate gill	*Terebellides.*
	With more than one gill	3.
3.	Thorax with more than 17 chaetigers	*Streblosoma.*
	Thorax with 17 chaetigers or less	4.
4.	Uncini pectinate	*Loimia.*
	Uncini avicular	*Pista.*

Genus ***PISTA*** Malmgren 1865

Thorax with 15–17 chaetigers; eye-spots may be present. One, two or three pairs of branchiae. Notopodial chaetae smooth; neuropodial uncini appear in the thorax on the 2nd chaetiger.

Pista grubei Augener, 1918

Pista grubei, Augener 1918, pp. 542–5, pl. 7, fig. 252–3, text-fig. 92.

LOCALITIES. Off Accra: Stn. 28 (1); Stn. 61 (1); Stn. 69 (1); Stn. 131 (1).

None of the specimens is complete, they vary between 25 and 47 mm. in length. There are 17 thoracic chaetigers, of which the first has only simple notopodial chaetae. In the next six segments there are also neuropodial groups of uncini in single rows, all the hooks lying in the same direction. The remaining 10 thoracic chaetigers, however, have the uncini lying alternately head to tail in a single row. The uncini are avicular in shape and all have a projecting basal process.

The gills are in two pairs, consisting of a long basal trunk supporting a mass of whorled branching filaments. They are dorsal, anterior to the first chaetiger.

DISTRIBUTION. Known also from Senegal, Ivory Coast, and French Congo.

Genus ***TEREBELLIDES*** Sars, 1835

With a single gill divided into four pectinate arms. Notopodial chaetae long, tapering and winged. Uncini of two types, the thoracic elongated, acicular, the abdominal pectinate.

Terebellides stroemi Sars, 1835

Terebellides stroemi, Fauvel, 1927*a*, pp. 291–2, fig. 100, *i–g*.
Terebellides stroemi, Fauvel, 1932, pp. 234–5.

LOCALITIES. Off Accra: Stn. 28 (4); Stn. 33 (2); Stn. 59 (4); Stn. 73 (2); Stn. 133 (2). Most of these specimens are complete, measuring between 10 and 30 mm. long. Buchanan Survey, 36·5 m. off Castle (1), 35 mm. in length.

Body rarely with more than 60 segments, the first 18 being thoracic, with the gill as above. Segments 3 to 6 have their anterior border free. Notopodial chaetae are simple and begin on segment 3; neuropodial uncini appear at the 6th chaetiger and are long, geniculate, acidular hooks; the remaining thoracic segments also have long uncini, but these end in blunt tips surmounted by small denticles. The abdominal uncini are avicular with a short base and transverse rows of teeth above the main fang.

Distribution. Mediterranean Sea, Atlantic Ocean, Indian and Pacific Oceans.

Genus *STREBLOSOMA* Sars, 1872

Body with a large number of segments; often with eyes; with two or three pairs of branchiae (sometimes five?) on the 1st, 2nd, or 3rd chaetigers. Notopodial capillary bristles appear on the 2nd segment (1st branchiate). Neuropodial uncini appear on the 5th segment (4th chaetiger).

Streblosoma persica (Fauvel), 1908

Grymaea persica, Fauvel, 1911, pp. 419–421, pl. 20, figs. 35–43.
Pseudothelepus nyanganus, Augener, 1918, pp. 552–555, pl. 7, figs. 257, 258, text-fig. 96.
Streblosoma persica, Fauvel, 1950, p. 384.

Localities. (1) Tenpobo shore, about 100 specimens collected in January, 1949, and February, 1951, measuring between 20–50 mm. in length. (2) Apam shore, 16.ii.49 (12). (3) Dixcove shore, 7.ii.51 (12). (4) Axim, 13/14.iv.49 (2).

The species is characterized by (*a*) a semi-circle of eye-spots on the dorsal surface of the tentacular disc and (*b*) the shape of the uncini, which have a large basal tooth, paired smaller median teeth and above these a single smaller tooth with several tiny ones on either side of it.

Notopodial chaetae occur on almost all segments. There are three pairs of branchiae, formed of numerous filaments, one pair on each side of the first three chaetigers. The first pair are based on transverse pads which form semi-circles around the anterior aspects of the notopodia of the first chaetiger. The remaining two are based on pads situated wholly on the dorsal side of the notopodia.

Distribution. The species has been recorded from the Persian Gulf, the Gulf of Manaar, the Island of St. Thomas in the Gulf of Guinea, Angola and Senegal.

Genus *LOIMIA* Malmgren, 1865

Body with 17 chaetigers and three pairs of aborescent gills. Anterior segments have lateral lobes. Notopodial chaetae winged. Uncini pectinate, opposed back-to-back in double rows from the 7th to the 17th thoracic chaetiger.

Loimia medusa (Savigny), 1822

Loimia medusa Augener, 1918, pp. 539–541, text-fig. 91.
Lanice fauvelii Day, 1934, pp. 71–73, fig. 14, *a–d*.

Locality. Off Accra, Buchanan Survey, in 36·5 metres off the Castle (1), an incomplete specimen of 34 chaetigers measuring 28 mm. in length.

The three pairs of gills, of which the first is very much the largest, all lie anterior to the first chaetiger. The uncini have 6 teeth in both thorax and abdomen.

Distribution. The species has been recorded from the English Channel, the Atlantic, Indian and Pacific Oceans, the Red Sea and the Persian Gulf.

Genus *AMAEA* Malmgren, 1865

Prostomium large, with many tentacles. Branchiae and eye-spots absent. Thorax of few segments, with notopodial chaetae. Abdomen consisting of an anterior achaetous portion and a posterior region with slender uncini.

Amaea accraënsis Augener, 1918

Amaea accraënsis Augener, 1918, pp. 561–562, pl. 7, fig. 246, text-fig. 98, from Accra.

This species has not been found in the present survey. The thorax has 11 chaetigers on the left hand side and 13 on the right. Notopodial chaetae are barbed capillaries. The achaetous abdominal region is about two-thirds as long as the thorax. There are 26–27 chaetigers posteriorly on the abdomen, bearing hooks with slightly bent tips. Augener's specimen measured 18 mm.

Distribution. This species is only known from the type specimen.

Family SABELLIDAE

Body divided into two regions: (*a*) thorax, with few segments, having notopodial capillaries and neuropodial uncini, and (*b*) abdomen, normally with numerous segments having notopodial uncini and neuropodial capillaries. Ventral glandular shields divided by a longitudinal groove. First chaetiger with an entire, or notched collar. Branchiae encircling the mouth. Tubes of mucous, or membranaceous or horny, material.

KEY TO GENERA

1. Thoracic neuropodia with a single row of avicular uncini, pickaxe-shaped chaetae absent . . . . 2.
   Thoracic neuropodia with a row of avicular hooks and a row of pickaxe-shaped chaetae (fig. 30, *a*) . . . . *Potamilla.*
2. Branchiae without dorsal stylodes . . . . *Laonome.*
   Branchiae with dorsal stylodes . . . . *Dasychone.*

Genus *LAONOME* Malmgren, 1865

Two symmetrical, semi-circular, branchial lobes not in the form of a spiral. Branchial filaments without stylodes. No pickaxe-shaped chaetae.

Laonome puncturata (Augener), 1918

Demonax puncturatus Augener, 1918, pp. 576–580, pl. 6, fig. 170, 171, text-fig. 102.
Euratella puncturata Monro, 1930, p. 203.

Localities. (1) Accra: considerable quantities of tubes were collected from Christiansborg shore on 15.i.49, 14.ii.49, and 17.iii.49. (2) Apam, 16.ii.49, numerous specimens and tubes. (3) Axim shore, 13/14.iv.49, numerous specimens but no tubes.

The prominent prostomial collar opens dorsally and forms two triangular lappets ventrally. There are between 10 and 12 branchial filaments which, in most specimens, bear at least one distinct pigment band. Pigment spots are also present on the collar and between the rami of thoracic and abdominal feet. No clear division is discernible between pigmented and non-pigmented forms since specimens from all localities show the above pattern, but one separate and large collection from Christiansborg shore (15.i.49) is completely without colour. The outside edge of the filaments is thickened in places suggesting rudimentary stylodes, but they are much less well developed than in the genus *Dasychone*. The branchial membrane reaches along one-sixth of the length of the branchial filaments ; the two palps are foliaceous and a little longer than the membrane.

There are 4–5 thoracic chaetigers and about 100 abdominal segments. Neuropodial uncini appear at the 2nd foot. Thoracic capillaries are of two kinds, short with a prominent limbate termination (not spatulate) and long with a slightly limbate end ; thoracic uncini are short, avicular. Abdominal capillaries and uncini are identical with thoracic bristles.

Augener (1918) placed this species in the genus *Demonax* Kinberg, which, however, has pickaxe-shaped chaetae in the thoracic neuropodia ; Monro, (1930) placed it in the genus *Euratella* Chamberlin, which has no collar and only one type of thoracic capillary. It is here considered that the species is referable to *Laonome*.

Genus ***DASYCHONE*** Sars, G.O., 1861

Both branchial lobes equal, not in the form of a spiral. Stylodes on the branchial filaments. Prominent collar. Pickaxe-shaped chaetae absent.

Dasychone lucullana (Delle Chiaje), 1828

Dasychone lucullana, Fauvel, 1927*a*, pp. 320–321, fig. 110, *m–s*.

LOCALITIES. Off Accra : Stn. 35 (1), 8 mm. long ; Stn. 73 (1), 15 mm. long ; Stn. 131 (1), 16 mm. long, all specimens complete.

The two branchial lobes are each made up of 13–14 filaments which carry slender, colourless stylodes dorsally. Along the filaments there are numerous violet pigment spots, which, when the branchiae are closed, give the effect of successive girdles of colour along the lobes. A small branchial membrane unites the bases of the gills ; there are two prominent canaliculate palps.

The body, other than the branchiate portion, is uniformly brown, with a small violet pigment spot between the parapodial rami. There are 8 thoracic and between 30 and 40 abdominal segments. Thoracic uncini which appear at the 2nd chaetiger, are avicular with slight extension at the base ; thoracic capillaries are limbate, short and long. Chaetae in the abdominal region are similar to thoracic types except that long capillaries, only slightly limbate, appear in far posterior segments.

DISTRIBUTION. Mediterranean and Adriatic Seas and from Senegal.

Genus ***POTAMILLA*** Malmgren, 1865

Branchial lobes symmetrical, not in a spiral, without stylodes. With a prominent, lobed collar. Thoracic notopodial capillaries limbate and spatulate, neuropodial chaetae avicular uncini and pickaxe-shaped. Abdominal notopodial uncini avicular and neuropodial capillaries limbate.

Potamilla casamancensis Fauvel, 1902

Potamilla casamancensis Fauvel, 1902, pp. 101–105, fig. 46–55, from the estuary of the River Casamance, Senegal.

LOCALITIES. Off Accra: Stn. 12 (1), complete, 16 mm. long; Buchanan Survey in 11 metres off Lighthouse (2), complete, 14 and 24 mm. long; Buchanan Survey in 5·5 metres off the Lagoon (1), incomplete, 8 mm. long.

There is an indentation in the collar dorsally, forming a deep groove which continues down the dorsal surface of the thorax; ventrally there is only a very slight break in the anterior border of the collar.

Ten to sixteen filaments make up each branchial lobe; the filaments are without eye-spots. There are 5–7 thoracic chaetigers; uncini and pickaxe-shaped chaetae appear at the second. The limbate capillaries on the first segment are in a longitudinal row, thereafter they are lateral. Spatulate capillaries appear at the second chaetiger and are normally few in number. Limbate capillaries are present in all segments, both thoracic and abdominal; spatulate chaetae have not been seen in the abdomen. Uncini in the thorax are avicular with long shafts; in the abdomen they are short.

DISTRIBUTION. *P. casamancensis* is only known through the above records.

Family SERPULIDAE

Body divided into two regions; (*a*) thorax, with few segments, having notopodial capillaries and neuropodial uncini, and (*b*) abdomen, with numerous segments, having notopodial uncini and neuropodial capillaries. First segment with a collar. With a thoracic membrane. Branchiae form a funnel around the mouth. Usually with an operculum. Tube calcareous.

KEY TO GENERA

1.	Body symmetrical	2.
	Body assymetrical. Tube spirally coiled	*Spirorbis.*
2.	Without an operculum	*Salmacina.*
	With an operculum	3.
3.	Chaetae of the first chaetiger bayonet-shaped with two basal stumps	4.
	Chaetae of the first chaetiger without basal stumps	5.
4.	Operculum simple, funnel-shaped	*Serpula.*
	Operculum compound, with a central crown of spikes	*Hydroides.*
5.	Operculum globular, transparent	*Apomatus.*
	Operculum horny, with a cylindrical or conical cap	*Vermiliopsis.*

Genus ***SALMACINA*** Claparède, 1868

Without an operculum and with few branchiae which are frequently bent distally. Uncini pectinate with a large inferior tooth.

Salmacina incrustans Claparède, 1868

Salmacina incrustans, Fauvel, 1927*a*, pp. 378–380, fig. 129, *l*.

Localities. Numerous specimens were collected from: (1) Tenpobo shore, on rocks, 4.ii.50; (2) Winneba rock face, sheltered side, 22.xi.49, forming compact masses about the Polyzoan, *Waterispora cucullata*; (3) Apam shore, 16.ii.49; (4) Axim hospital reef, 13.iv.49, L.W.M., some specimens were present on a tube of *Sabellaria spinulosa* var. *alcocki*.

The majority of these specimens measure between 2 and 3 mm. Tubes are white, cylindrical in shape, and very fragile.

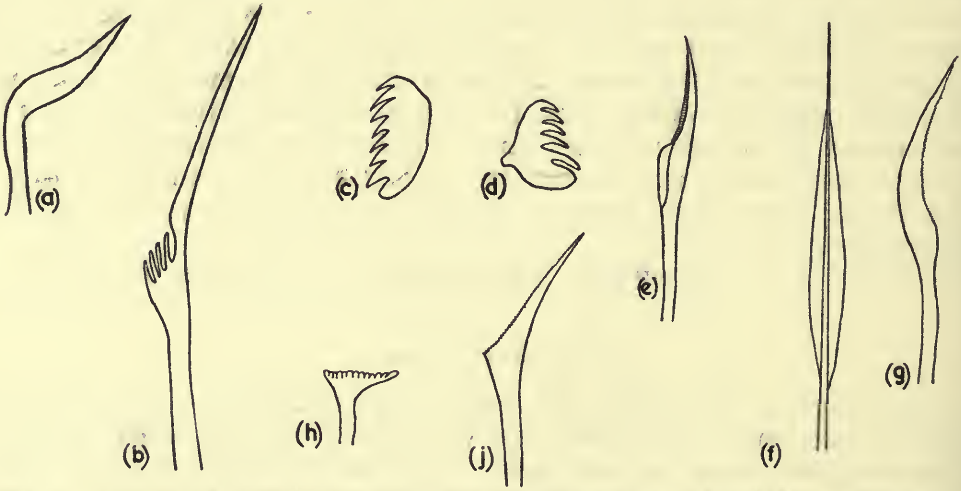

Fig. 30. Chaetae of (*a*) *Potamilla casamancensis*, pickaxe-shaped bristle from a thoracic neuropodium, × 350 (stn. 49); (*b*) *Salmacina incrustans*, a notopodial chaeta from the first thoracic segment × 200, (Winneba); (*c*) and (*d*) *Hydroides arnoldi*, thoracic and abdominal uncini respectively, × 400 (*e*), (*f*) and (*g*) *Apomatus similis*: (*e*) *Apomatus*-type chaeta from a posterior thoracic segment, × 100, (*f*) limbate chaeta from a thoracic segment, (*g*) scythe-like chaeta from a median abdominal segment × 150; (*h*) *Serpula vermicularis*, trumpet-shaped abdominal chaeta, × 200 (Stn. 115); (*j*) *Vermiliopsis multicristata*, geniculate abdominal chaeta, × 200.

There are four pairs of gill filaments and seven thoracic chaetigers. A notopodial chaeta from the first of these is shown in Text-fig. 30, *b*. This form is characteristic for the species.

Distribution. Mediterranean Sea and Atlantic Ocean.

Genus *HYDROIDES* Gunnerus, 1768

Chaetae of the first chaetiger bayonet-shaped, with two humps at the base of the blade. Thoracic chaetae limbate ; abdominal chaetae trumpet shaped. Uncini in thorax and abdomen with coarse teeth. Operculum funnel-shaped, with radii ending bluntly or in fine points, and with a crown of horny spines rising from its centre.

Pixell (1913) suggested that *Hydroides* should include those species with opercular spines having lateral processes and that species devoid of these lateral processes should be included within the genus *Eupomatus*. This division is not adopted in this paper.

Key to Species

1.	Opercular spines all alike	2.
	Opercular spines not all alike	*H. spinosus.*
2.	Opercular spines with lateral processes	*H. norvegica.*
	Opercular spines without lateral processes	*H. arnoldi.*

Hydroides norvegica Gunnerus, 1768

Hydroides norvegica, Fauvel, 1927*a*, pp. 356–7, fig. 122, *i–o*.

Locality. Scraped off copper sheathing of boat and body, Gold Coast, (50).

The species is immediately recognizable by its opercular structures. The basal disc is soft and white, bearing marginally between 20 and 30 crenulations. Frequently the distal horny disc is missing but, when present, it carries 13 to 15 large spines with smaller lateral ones. A small vertical spine is situated in the centre of the opercular disc. The operculum itself is a modified branchial filament, the ventralmost of one side or the other ; whichever it may be, and there is no constancy, the other is always broken off.

Chaetae of the first of the seven thoracic chaetigers have two humps below the terminal point and below the humps there are a few fine denticulations. Thoracic uncini have seven teeth and abdominal uncini five.

Distribution. Cosmopolitan.

Hydroides spinosus (Pixell), 1913

Eupomatus spinosus Pixell, 1913, p. 78, pl. 8, fig. 5.

Localities. (1) Tenpobo, No. 1 Reef, 21.xi.49 (1), complete, 15 mm. long. (2) Off Accra : (*a*) Trawled 2 miles west of Densu River, 2.iii.49 (1), incomplete, 10 mm. long ; (*b*) Stn 99 (3), one complete, 10 mm. long, on tubes of *Turritella annulata* Kiener ; Stn. 127 (1), complete, 11 mm. long, on a tube of *T. annulata*.

These specimens differ only slightly from the original description (Pixell, 1913). Thus the basal disc has frequently more than 32 long, pointed teeth and the number of tall strong spines on the upper disc, is not constantly 11 but varies, some specimens having 8, 9 or 10. The shape of all the spines except one is identical, they each have a terminal hook pointing outwards, a near-terminal one pointing downwards and inwards and an inner median near the base. The exceptional one is longer than the others, curves over them, and has only a basal hook.

Distribution. *H. spinosus* has previously been recorded from the Suez Canal area and the Cape of Good Hope.

Hydroides arnoldi Augener, 1918

Hydroides arnoldi Augener, 1918, pp. 595–598, text-fig. 107, pl. 6, figs. 151, 152, from Togo, Dahomey, and the Island of Annobon.

Locality. Axim shore, 14.iv.49 (3), incomplete, 4–11 mm. long.

There are seven opercular spines which have an inner basal hook but are devoid of other processes. The largest, and possibly oldest, specimen has almost straight spines with blunt ends (Augener, 1918, pl. 6, fig. 152), but the smallest, and possibly youngest, has spines ending in a curved tip. It is suggested that normal wear on the operculum has produced these different shapes and the species may be expected to vary in this character even more than is noted here.

Thoracic and abdominal uncini are illustrated in Text-fig. 30, *c* and *d*.

Distribution. *H. arnoldi* is only known from the above records.

Genus ***APOMATUS*** Philippi, 1844

With a globular transparent operculum. Branchial filaments with eye-spots and short connective membrane. No special notopodial chaetae on the first thoracic segment, which is without neuropodia, but with characteristic *Apomatus*-type bristles on the last segments (Text-fig. 30, *e*).

Apomatus similis Marion and Bobretzky, 1875

Apomatus similis, Fauvel, 1927*a*, pp. 385–387, fig. 131 *k–p*.

Locality Off Accra, Stn. 115 (10), with tubes, on the Polyzoan *Steganoporella buskii* Harmer. The specimens measure up to 6 mm. in length.

The branchial lobes are made up of 10 to 16 filaments each. The second dorsal filament carries a globular transparent operculum distally, but it is otherwise unmodified and combines a branchiate and operculate function. This represents a primitive stage in the modification of a branchial filament to an operculum. Complete modification is found in the majority of Serpulidae, but there is no trace of it in *Filograna* and *Protula*.

There are seven thoracic and well over 60 abdominal segments. The majority of thoracic chaetae are limbate (Text-fig. 30, *f*), but in the last 3–4 segments of the thorax characteristic *Apomatus*-type bristles appear (Text-fig. 30, *e*). Anterior abdominal segments are achaetous. Neuropodia in the middle of the abdomen have very small scythe-like chaetae (Text-fig. 30, *g*), but in four posterior segments long capillaries are present. Abdominal and thoracic uncini are alike, with numerous small teeth and a long basal one.

Tubes are white and semi-cylindrical, with slight lateral crenulations.

Distribution. English Channel, Mediterranean Sea, Atlantic Ocean.

Genus ***SERPULA*** Linnaeus, 1758

Chaetae of the first thoracic segment bayonet-shaped, with two humps at the base of the blade. Operculum funnel-shaped with radii ending bluntly along the margin. Thoracic chaetae limbate, abdominal chaetae trumpet-shaped. Uncini with few, but stout teeth.

Serpula vermicularis Linnaeus, 1767

Serpula vermicularis, Fauvel 1927*a*, pp. 351–352, fig. 120, *a–q*.

LOCALITIES. (1) Tenpobo reef, 12.xi.49 (2), incomplete, 10 and 20 mm. in length, without tubes. (2) Off Accra, Stn. 115 (3), complete, up to 20 mm. in length.

These specimens appear to be smaller than is normal for the species (Fauvel, 1927*a*), but those from Stn. 115 were taken from tubes completely attached to the polyzoan, *Steganoporella buskii*, none of the tubes growing free, and they may be juveniles. The tubes are pink in colour, and triangular in shape with a prominent dorsal keel.

There are 16–20 branchial filaments in each lobe united by a short basal membrane. The first dorsal filament of one side is completely adapted as an operculum, with a funnel-shaped termination having a crenulated surface. The first dorsal filament on the opposite side to that bearing the operculum is partially modified ; it is similar to the opercular filament, but is smaller and lacks the funnel-like termination.

There are seven thoracic chaetigers the first without neuropodia. Apart from the bayonet-shaped chaetae with two basal humps on the first thoracic segment, notopodial-chaetae are unmodified capillaries. Abdominal neuropodial chaetae are trumpet-shaped (Text-fig. 30, *h*).

DISTRIBUTION. Cosmopolitan.

Genus ***VERMILIOPSIS*** St. Joseph, 1906

Operculum a horny cylindrical or conical cap. No special chaetae on the first chaetiger, which is without neuropodia. *Apomatus*-type chaetae in posterior thoracic segments. Abdominal chaetae geniculate (Text-fig. 30, *j*).

KEY TO SPECIES

1. With seven thoracic chaetigers . . . . *V. multicristata.*
2. With nine thoracic chaetigers . . . . *V. prampramiana.*

Vermiliopsis multicristata (Philippi), 1844

Vermiliopsis multicristata, Fauvel, 1927*a*, pp. 365–366, fig. 125, *k–s*.

LOCALITY. Off Accra, Stn. 115 (6), some complete, up to 10 mm. long, taken from tubes attached to the polyzoan *Steganoporella buskii*.

This species is characterized by its tube bearing 5–6 longitudinal ridges. There are about 10 branchial filaments to each lobe. The operculum is horny and cylindrical to conical in shape. In the thorax there are seven chaetigers and in the abdomen upwards of 50. The majority of thoracic chaetae are limbate, but in posterior segments a few *Apomatus*-type bristles appear. Abdominal chaetae are short and geniculate (Text-fig. 30, *j*) anteriorly, but posteriorly long capillaries appear.

Distribution. Mediterranean Sea and Atlantic Ocean—Madeira and the Azores.

Vermiliopsis prampramiana Augener, 1918

Vermiliopsis prampramiana Augener, 1918, pp. 603–604, pl. 7, fig. 256, from Pram Pram.

This species is only known through this record, and is the only species of *Vermiliopsis* known with nine thoracic chaetigers. Augener's description is otherwise incomplete, and it is difficult to assess the species relationship with other members of the genus or family.

Genus ***SPIRORBIS*** Daudin, 1800

Body assymetrical, with less than five thoracic segments. Opercular peduncle without pinnules. Tubes spirally coiled, dextral or sinistral.

Key to Sub-genera

1.	Tube dextral	*2.*
	Tube sinistral	*3.*
2.	With 4 thoracic segments	(*Paradexiospira*).
	With 3 thoracic segments	(*Dexiospira*).
3.	With 4 thoracic segments	(*Paralaeospira*).
	With 3 thoracic segments	*4.*
4.	Chaetae of the first thoracic chaetiger limbate	(*Leodora*).
	Chaetae of the first chaetiger with a crenulated wing	(*Laespira*).

This genus was, surprisingly, absent from the collections, but it is almost certainly present in the Fauna, and, for this reason the above key has been included, (from Fauvel, 1927*a*, pp. 389–391). Augener (1918, pp. 607–608), reported *Spirorbis* sp. from the "Cape Coast Castle", probably Christiansborg Castle, but his description does not permit further identification. When, and if, species are collected further reference to Fauvel should be made.

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GRACE E. PICKFORD

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PART I.—FURTHER LIGHT ON THE OCTOPUS RUGOSUS PROBLEM

By GRACE E. PICKFORD

IN spite of the efforts of Robson (1929), which form a landmark in the history of octopodan taxonomy, the *Octopus rugosus* problem remains unsolved, an outstanding source of confusion obscuring the correct identification of small, rough, *vulgaris*-like specimens from all parts of the world. Some years ago the writer reviewed the western Atlantic forms which had been, or could be, assigned to *Octopus rugosus*. It was possible to show that no such species can be found in American waters and that western Atlantic specimens previously referred to it were either *O. vulgaris* or, occasionally, belonged to one of the other Caribbean species (Pickford, 1945, 1946).

It is believed that the problem can best be solved by a zoogeographical approach, *pari passu* with increasing knowledge of each local fauna to the point that makes the recognition of its component species a matter of certainty. Through the work of Voss (1950, 1951, etc.) and the author we have now arrived at this state of knowledge of the American east coast fauna. However, the situation in other parts of the world is less satisfactory. Octopodan taxonomy has always been hampered by the lack of adequate series of specimens collected from any one locality and this, together with the confusing effects of different states of preservation, has made recognition of the limits of variation within a single species all but impossible.

In the present contribution an attempt has been made to clarify the status of those specimens from the eastern Atlantic and South Africa which Robson identified as *O. rugosus* and which are now in the collections of the British Museum. A survey of bodily characteristics, irrespective of species assignation, is given in Table I. It will be seen that only 7 of the 22 specimens are sexually mature, 4 are well grown but immature, and 11 are juvenile. In a difficult problem of this nature it is obvious that no definite conclusions can be based on juvenile, nor even on sexually immature specimens, except in so far as they can reasonably be assigned to adult forms with well established characteristics.

Octopus rugosus, as it is generally understood, is a species closely resembling *O. vulgaris* but smaller in size ; the head is broader, the arms shorter, and the rough, finely granulated skin is darkly reticulated with black. None of these characters, taken singly, can be used with any degree of certainty for the separation of the two species. Taken together the resulting picture is indistinguishable from that of juvenile and immature specimens of *O. vulgaris*, so that it may be conjectured that *O. rugosus* is merely the young of *O. vulgaris* (Pickford, 1945). This point of view is that taken by the writer who believes that it is necessary to *prove* that an Atlantic specimen assigned to *O. rugosus* is not a young *O. vulgaris* before it can be considered to belong to any other species ; a *rugosus*-like specimen should be assigned to *O.*

vulgaris unless there is conclusive evidence that it does not belong to this species. Robson, on the other hand, used the name *O. rugosus* as a hold-all to receive those *vulgaris*-like specimens about whose identification he was uncertain and, as a result of this policy, it is not surprising to find that the majority of his eastern Atlantic specimens, as indicated above, are juvenile or immature.

We may approach the problem from another angle. Bosc's *Sepia rugosa* came from Senegal and the type is lost. Lamarck (1799) gives no locality for the two specimens to which he gave the name *O. granulatus*. He points out that this species may be merely a variety of *O. vulgaris* and concludes that it is probably the same as Bosc's *rugosus*. The types are lost and, in the absence of evidence to the contrary, it appears advisable to relegate the name *O. granulatus* to the synonymy of *O. vulgaris*. A similar conclusion is probably justified in the case of *O. tuberculatus* Blainville, the type of which is also lost. However, since the species is from Sicily, its status should be re-examined in connexion with a more thorough taxonomic study of the Mediterranean population.

It must be pointed out that the original specimens of *O. rugosus* and *O. tuberculatus*, not to mention numerous other specimens referred by various authors to these species or to *O. granulatus*, were reported from geographical areas in which *O. vulgaris* is known to occur. Therefore, *O. rugosus* (to confine the discussion to one of the three problematical forms) is *not* a geographical race or subspecies of *O. vulgaris*. Either it is a distinct species or it is inseparable morphologically from the extremes of the *O. vulgaris* population. This is an important consideration. If two species occur together in the same geographical area they must form two separate breeding populations.

The search for *O. rugosus* is therefore the search for a West African *vulgaris*-like sibling species which is distinct as a breeding population from *O. vulgaris* with which it is sympatric. As the result of previous investigations (Pickford, 1945, 1946) it can definitely be stated that *O. rugosus* does not occur in the western Atlantic but the problem of Indo-Pacific forms that have been assigned to this species awaits further clarification. However, if the existence of a true *O. rugosus* cannot be established in the eastern Atlantic it is highly improbable that anything recorded from Indo-Pacific waters could legitimately be assigned to this species.

The study of the British Museum specimens reviewed below leads to the following conclusion :

(1) Nearly all specimens from the eastern Atlantic are probably or certainly referable to *O. vulgaris*. It is probable that the correct assignation of the juvenile specimens will always remain in doubt but 6 of the 7 adults present no features which would permit their separation from *O. vulgaris*.

(2) Among the series there is one juvenile specimen from Madeira that has a distinctive pattern of zebra bands on the arms. Although the characteristics (Table I, B.M., 1898.5.10.2) are similar to those of *O. vulgaris* the correct assignation of this specimen must remain in doubt.

(3) One specimen from the Cape Verde Islands (1889.4.24.17), a mature male, certainly represents a distinct species on account of the length of the ligula which is quite outside the range for *O. vulgaris*. A similar male and also a female that

apparently belong to the same species have been described by Adam (1952) from the Cape Verde Islands as *Octopus* sp. The question arises whether these individuals should be arbitrarily assigned to *O. rugosus*, with which they show some general agreement, or whether it would be preferable to designate them by a new name. The original description of *O. rugosus* does not permit recognition with any degree of certainty. Bosc's figures (1792, Figs. 1 and 2), if correctly drawn, show an animal of 42 mm. mantle-length with moderately long arms (MAI 32) and an unusually shallow web (WDI 13·5); the suckers are of moderate size (SnI 9·5) but none are specially enlarged. In favour of assigning the Cape Verde specimens to this species is the geographical area from which it came, as well as the general appearance and bodily proportions, except for the shallow web. The only contrary evidence is the shallow web and the uncertainty whether Bosc's *O. rugosus* was not, after all, just a young *vulgaris*. For the sake of clarity and to avoid the confusion that might result from the use of a name which is, by now, so clouded in obscurity, it has seemed preferable to propose a new name for this Cape Verde species.

(4) The problem of the specific affiliation of the South African *rugosus*-like population remains unsettled. The individuals that have been examined, from the Cape Province and Natal, appear to belong to the same species and to represent a moderately uniform group. Robson admits (1929, p. 59) that true *O. vulgaris* occurs in South African waters. The two males, from Port Elizabeth and from Natal respectively, have the characteristic minute ligula of *O. vulgaris*.[1] Massy (1925) found the same feature in males which she identified as *O. granulatus* in the collections of the Natal Museum (LLI 1·7 and 1·65 respectively, calculated from her measurements). There is a small but possibly significant detail regarding the repeated reversal of the direction of coiling of the horn in the spermatophore of one of the males (B.M., 1890.9.4.4), but our information concerning the range of variation in spermatophores of *O. vulgaris* is inadequate to assess this feature. Also the females, with ripe ovaries, are unusually small for sexually mature females of *O. vulgaris*; but this again amounts to no more than a suggestion. Possibly the South African forms represent a geographical race or subspecies of *O. vulgaris* with these slightly different features. Such a conclusion could only be confirmed by the statistical analysis of a long series of specimens.

A detailed account of the specimens follows:

DISCUSSION OF SPECIMENS WHICH ARE PROBABLY OR CERTAINLY REFERABLE TO *OCTOPUS VULGARIS* LAM.

ENGLISH CHANNEL

(1) B.M., 1927.2.10.2. *Octopus rugosus* (Bosc), Robson (1929). Plymouth. C.92.

It was pointed out in a previous paper (Pickford, 1946) that this specimen is clearly a female of *O. vulgaris*. I take this opportunity to publish the characteristics listed in Table I and to call attention to the following features: the arms are unusually short and the web rather deep but the suckers and gills are normal; there is a very conspicuous lateral seam round the mantle, no doubt an accident of preservation; the ovary is quite small and the ova are minute.

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[1] Attention must again be called to Robson's mistake in tabulating the ligula-length indices for *O. vulgaris*. It appears that in this one case he referred the length of the ligula to the mantle length instead of to the length of the hectocotylised arm, thus giving misleadingly high values (see Pickford, 1945).

TABLE I.—*Characteristics of specimens from the eastern Atlantic, and South Africa which were referred by Robson* (1929) *to the species* Octopus rugosus (*Bosc*), *in the collections of the British Museum.**

B.M. No.	Sex	ML	MWI	HWI	MAI	WDI	SnI	Gill
English Channel								
1927.2.10.2	♀ imm.	70	79	51	49	39	14·3	11
Mediterranean								
1867.3.27.9	♂ juv.	21	67	72	35	15	8·6	8·5
Madeira								
1898.5.10.2	♀ imm.	32	78	69	27	21	11·0	*ca.* 8
1912.12.31.118	juv.	8	—	—	—	—	—	—
1912.12.31.119	juv.	6·5	—	—	—	—	—	—
Canary Islands								
1954.2.25.1	juv.	8·5	—	—	—	—	—	—
1954.2.25.2	juv.	8	—	—	—	—	—	—
1954.2.25.3	juv.	6	—	—	—	—	—	—
Cape Verde Islands								
1851.1.24.1	♀ imm.	50	84	70	28	24	16	8
1855.9.29.2	♂ juv.	31	68	56	31	21	9·7	*ca.* 8
1889.4.24.17	♂ mat.	24	92	71	40	28	8·3	9
Ascension								
1889.4.24.14	♀ imm.	57	88	73	32	28	14	*ca.* 10
		(55)†	(91)	(73)	(24)	—	(12·7)	—
West Africa								
1928.3.17.1	♂ mat.	24	58	63	21	21	16·7	*ca.* 6–7
1928.3.17.2	juv.	13	46	62	—	—	11·5	—
1928.3.17.3	juv.	15	93	—	—	—	15·3	—
1889.4.24.15	juv.	7·5	—	—	—	—	—	—
South Africa								
1890.9.4.4	♂ mat.	30	77	74	27	23	15	8·5
1924.9.9.11	♂ mat.	41	—	—	—	—	—	—
1924.9.9.12	♀ mat.	45	—	—	—	—	—	—
1924.9.9.13	♀ mat.	59	—	—	—	—	—	—
1926.10.20.30	♀ mat.	27	—	—	—	—	—	—
		(28)‡	(86)	—	(34·5)	—	(10·7)	—
1889.4.24.18	juv.	12	—	—	—	—	—	—

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* Two females from the "South Coast" could not be found (B.M., 1872.2.3.12–13). Three specimens (1865.5.23.1) from an unknown locality omitted. Data based on new measurements unless otherwise indicated. Symbols as in Pickford (1945).

† Data from Hoyle (1886).

‡ Data from Massy (1927).

MEDITERRANEAN

(2) B.M., 1867.3.27.9. *Octopus rugosus* (Bosc), Robson (1929). Mediterranean, purch. of Mr. Cutter. C.104.

This is a very young male, not a female as listed by Robson. As far as can be determined it is probably referable to *O. vulgaris*.

MADEIRA

(3) B.M., 1898.5.10.2. *Octopus rugosus* (Bosc), Robson (1929). Porto Santo, Madeira, H. S. Wellcome Esq. C.86.

This specimen, an immature female, is remarkable for its coloration. There are light and dark zebra bands on the arms and it is very dark and blotchy on the back and head. The ovary is undeveloped but has moved to a ventral position and is possibly rather advanced for a *vulgaris* of this size ; the ova are minute. The jaws have been dissected out and the radula is mounted on a slide. The bodily proportions are similar to those of a typical *vulagris* but on account of the peculiar coloration I hesitate to refer the animal to this species. It will be necessary to await further collections from this region to establish the existence of a form with banded arms and, until such time, it may be considered to be merely an unusual specimen of *O. vulgaris*.

(4) B.M., 1912.12.31.118 and 119. *Octopus rugosus* (Bosc), Robson (1929). Pedro de Malha, Porto Santo, Madeira, 60 fathoms, R. Kirkpatrick Esq. C. 152–153.

Two very young specimens with the characteristic rhomb of 4 papillae on the back commonly seen in juvenile specimens of *O. vulgaris* ; probably correctly referred to this species.

CANARY ISLANDS

(5) B.M., 1954.2.25.1–3. *Octopus rugosus* (Bosc), Robson (1929). Canaries, R. McAndrew. C. 100–102.

Three very young specimens, probably all referable to *O. vulgaris*. The two larger specimens each have the characteristic rhomb on the back.

CAPE VERDE ISLANDS

(6) B.M., 1851.1.24.1. *Octopus rugosus* (Bosc), Robson (1929). St. Jagos, C. de Verd, Ch. Darwin Esq., No. 122. C. 85.

An immature female, very dark, mottled and rough. The ovary is small and apical ; the ova minute. The jaws have been dissected out. The suckers are large, as in *vulgaris*, the arms moderately long and the web moderately deep. There seems to be no reason why this specimen should not be assigned to *O. vulgaris*.

(7) B.M., 1855.9.29.2. *Octopus rugosus* (Bosc), Robson (1929). St. Vincent, Mr. MacGillivray coll. C. 119.

This specimen is an immature male. The head is rather warty, the body smooth. The total absence of a hectocotylus at a mantle-length of 31 mm. indicates that it belongs to a large species and there seems to be no reason why it should not be assigned to *O. vulgaris*.

ASCENSION

(8) B.M., 1889..4.24.14 *Octopus occidentalis* Hoyle (Steenstrup MS), Hoyle (1886); *Octopus rugosus* (Bosc), Robson (1929). Challenger Coll., Ascension, April 1878. C. 69.

This specimen, an immature female, is the *type* of *O. occidentalis* and was described by Hoyle (1886) in the Challenger Reports. In its present state it is very dark and hard. A comparison of its present measurements with those given by Hoyle (Table I) indicate that a very considerable shrinkage of the arms has taken place during sixty years of preservation (the specimen was examined by me in 1946) but the length and proportions of the mantle and head are little changed. The longest arm, the second left, now measures about 180 mm. whereas Hoyle gives a length of 230 mm. No doubt his measurements, which represent the condition of the specimen when it was in a better state of preservation, should be accepted.

Robson could find no reason why this specimen should not be assigned to *O. rugosus* and I can see no reason why it should not be assigned to *O. vulgaris*.

WEST AFRICA

(9) B.M., 1928.3.17.1. *Octopus rugosus* (Bosc), Robson (1929). Old Collection (Rich), West Africa. Bears manuscript name " Octopus rugosus var. longimanus. Type." C. 260.

This is a mature male, very dark in color. The bodily proportions are those of *vulgaris* (Table I) the ligula (Table II) is minute and typical of *vulgaris*. The gills are very damaged and the low estimate of the number of gill lamellae may be due to this condition. Spermatophores were removed from Needham's organ; the length (9 mm.) gives an index of 37·5, which is typical of *vulgaris*. The horn is very slender and measures about 4 mm. in length; there are 40 to 50 spiral turns, partly uncoiled; only the distal extremity of the horn, proximal to the middle piece, is not coiled. This last mentioned feature is not characteristic of a well preserved spermatophore of *vulgaris* but the partial uncoiling and poor state of preservation may well account for such a condition (compare Adam, 1952, Fig. 53B). There seems to be no reason why this specimen should not be assigned to *O. vulgaris*.

(10) B.M., 1928.3.17.2. *Octopus rugosus* (Bosc), Robson (1929). Sierra Leone, W. P. Lowe. Bears manuscript name " Octopus rugosus ? var. longimanus." C. 262.

A juvenile specimen, rather warty, with 4 dorsal papillae in a rhomb on the back. Probably referable to *O. vulgaris*.

(11) B.M., 1928.3.17.3. *Octopus rugosus* (Bosc), Robson (1929). Murray Town, Sierra Leone, W. P. Lowe. C. 371.

This juvenile specimen is very dark and extremely hard and shrunken. It is very probably a young *vulgaris.*

(12) B.M., 1889.4.24.15. *Octopus tuberculatus* Blainville, Hoyle (1886); *Octopus rugosus* (Bosc.), Robson (1929). Challenger Coll., No. 122B, off Barra Grande, Lat 9° 9′ S., Long. 34° 53′ W., depth 32 fm, red mud, 10.ix.1873. C. 115*a.*

This specimen was identified as *O. tuberculatus* by Hoyle, but is not described. There are indications of the dorsal rhomb of papillae and the specimen is very probably referable to *O. vulgaris.*

SOUTH AFRICA

(13) B.M., 1890.9.4.4. *Octopus rugosus* (Bosc), Robson (1929). Port Elizabeth, South Africa, H. S. Spencer. Bears manuscript label "*Octopus granulatus* Lam." C. 108.

A mature male with all the characteristics of *O. vulgaris.* The specimen is very hard but one spermatophore was recovered from Needham's organ and was found to be in a moderately good state of preservation. Its length (10·5 mm) gives an index that is typical of *vulgaris* (Table II). There are about 37 coils to the spiral horn, interrupted by two irregular regions of partial uncoiling. The direction of the spiral is reversed several times, as follows: 8 coils anticlockwise, about 6 irregular clockwise coils, an irregular break, 3 anticlockwise coils followed immediately by 5 clockwise turns, an irregular break, 8 anticlockwise coils followed by 6 clockwise. This repeated reversal of the spiral is not a characteristic feature of *vulgaris* spermatophores but there has been no large scale survey of spermatophore variation in this species and, in the absence of such data and of an adequate series of spermatophores from South African males, it seems unwise to attach any great significance to the condition. Apart from this feature the specimen appears to be a typical *O. vulgaris.*

TABLE II.—*Characteristics of adult male specimens referable to* Octopus vulgaris *Lam.**

B.M. No.	LLI	CLI	PLI	SpLI	Horn Coils
West Agrica					
1928.3.17.1	1·8	28	18·7	37·5	40–50
South Africa					
1890.9.4.4	0·9	50	16·7	35	*ca.*37
1924.9.9.11	1·8	30	—	—	—

* Symbols as in Pickford (1945).

(14) B.M., 1924.9.9.11–13. *Octopus rugosus* (Bosc), Robson (1924 and 1929). Natal, Gilchrist Stns. 388 and 389. C. 105–107.

These specimens were identified but not described by Robson. The male has a minute ligula (Table II) and is apparently a typical *vulgaris*; there is one broken spermatophore in Needham's organ but it was not removed. The two females have ripe ovaries with small eggs. The specimens are rather small in size for sexually mature females of *vulgaris* but are apparently referable to this species and resemble the male with which they were associated.

(15) B.M., 1926.10.20.30. *Polypus granulatus* (Lamarck), Massy (1927) ; *Octopus rugosus* (Bosc), Robson (1929). Cape Colony, South African Museum 1311D. C. 109.

This female was described by Massy and indices based on her measurements are given in Table I. The specimen closely resembles the South African specimens from Natal, listed above, and similarly can be referred, in all probability, to *O. vulgaris*.

(16) B.M., 1889.4.24.18. *Octopus granulatus* Lam., Hoyle (1886) ; *Octopus rugosus* (Bosc), Robson (1929). Challenger Coll., Simon's Bay, Cape of Good Hope, 10–20 fms. C. 114.

A very young specimen, with dorsal papillae in a characteristic rhomb, very probably referable to *O. vulgaris*.

In addition to the specimens listed above Robson's *type* of *Octopus rugosus* var. *sanctae helenae* (B.M., 1868.3.12.1) was examined but nothing new can be added to the original description (Robson, 1929). Although it is a badly distorted specimen with somewhat deceptive features there seems to be no valid reason why it should not be assigned to *O. vulgaris*. The same is true also of *Octopus verrucosus* Hoyle (1886) (B.M., 1889.4.24.16). The *type* of this species was fully redescribed by Robson (1929) who states that " It seems to exhibit characters of *O. vulgaris* and *O. rugosus* in combination with individual peculiarities." The distinctive features listed by Robson do not appear to be sufficiently diagnostic to justify recognition of this species as distinct from *O. vulgaris*.

The following summary is offered to clarify the present synonymy of *O. vulgaris*, in the light of the considerations outlined above.

Octopus vulgaris Lamarck

Octopus vulgaris, Robson (1929). All specimens from the north-eastern, north-western, central and south Atlantic, and from West and South Africa, which Robson refers to this species must be accepted as correctly identified. Specimens from the Indo-Pacific require further confirmation.

Octopus rugosus, Robson (1929). The majority of specimens from the eastern, western, central and south Atlantic, and from West and South Africa which Robson referred to this species are probably correctly assigned to *O. vulgaris*. It cannot be established that *O. rugosus* is a valid species. Some American specimens are referable to *O. briareus* Robson, and *O. joubini* Robson (Pickford, 1945, 1946), and one specimen from the Cape Verde Islands, described as a new species in the present contribution, must be excluded.

Octopus rugosus var. *sanctae helenae*, Robson (1929) = *O. vulgaris*.

Octopus verrucosus, Hoyle (1886), Robson (1929) = *O. vulgaris*.

Octopus vulgaris, Pickford (1945, 1946). The proposed synonymies of western Atlantic species appear to remain valid. *O. geryonea* Gray, *O. eudora* Gray, *O. filosus* Howell, *O. carolinensis* Verrill, and various other obscure western forms are assimilated into the synonymy of *O. vulgaris*.

Octopus vulgaris, Adam (1952). Probably all the West African specimens which Adam referred to this species are correctly assigned. No doubt would arise if it were not for the two specimens listed from the Cape Verde Islands, but not identified, which must be placed in a new species (see below).

There is an urgent need for the re-examination of specimens assigned either to *O. vulgaris* or to *O. rugosus, granulatus* or *tuberculatus* from the Indo-Pacific. As Robson has pointed out, the ligula of oriental specimens of *O. rugosus* (as understood by him) differs from that of Atlantic specimens ; the average size is larger and the calamus shorter. A consideration of the data, so carefully assembled by Robson, appears to indicate that the Indo-Pacific *rugosus*-complex is composite in character and distinct from the Atlantic *rugosus*-complex. It is difficult to understand why he discarded this interpretation but one factor was the confusion that arose due to the inclusion of western Atlantic species that are not *O. vulgaris* in the synonymy of *O. rugosus*. The range of variation in critical characters, such as the length of the ligula, was thus enlarged in such a manner as to obscure the true situation.

Octopus vincenti n. sp.

Octopus granulatus (part), Hoyle (1886).
Octopus rugosus (part), Robson (1929).
Octopus sp., Adam (1952).

Holotype : Iles du Cap-Vert, 28.x.1948, Exped. Oceanogr. Belge côtes africaines de l'Atlantique Sud. Inst. Royal Sci. Naturelles de Belgique.

SPECIMEN EXAMINED :

B.M., 1889.4.24.17. *Octopus granulatus* Lam., Hoyle (1886) ; *Octopus rugosus* (Bosc), Robson (1929). Challenger Coll., St. Vincent, Cape Verde Islands, 25.iv.1876, depth 15–20 fms. C. 118.

In 1952 Adam listed a male and female from the Cape Verde Islands which were obviously different from *Octopus vulgaris*, but to which he hesitated to give a new name. The length of the ligula in the male is quite outside the range of *vulgaris* and the horn of the spermatophore is straight, without indications of uncoiling (Adam, Fig. 53D). These two features alone are sufficient to justify the recognition of a new species since no such males have hitherto been described from the eastern Atlantic. In addition the animal is of small size, mantle length 25–29 mm., the arms are short, the web deep and the suckers small, close to the lower limits for *O. vulgaris*. The female has a similar combination of characters but, on account of the great variability of *Octopus vulgaris*, Adam concluded that it was not possible to recognise the female as a distinct species.

During the course of the present investigation it was discovered that the male listed above, in the Collections of the British Museum, presented the same combination of characters. It was identified by Hoyle as *O. granulatus* and referred by Robson to *O. rugosus*, but under no circumstances can it be placed, along with other eastern Atlantic specimens of Robson's *rugosus* list, in the synonymy of *O. vulgaris*.

The size of the ligula alone precludes such an identification. The similarity to Adam's male is so great that there can be no doubt that the two specimens are conspecific. The only special feature of the British Museum specimen is the presence of a faintly darker area in front of the eye, about 4 mm. in diameter, which could possibly be interpreted as the remains of a faded ocellus ; but this interpretation seems unlikely.

The British Museum specimen is not sexually mature and, in view of the highly distinctive spermatophores of Adam's specimen, which were in a good state of preservation and have been carefully figured, it seems preferable to designate this male as the *holotype*. The female, also from the Cape Verde Islands and with similar bodily features, is almost certainly referable to the same species but caution dictates that it should not be designated as the gynotype. It is unfortunate that the ovary was not sufficiently advanced for the size of the eggs to be determined.

The bodily proportions and characteristics of the three specimens are summarized in Table III. Adam did not describe either the funnel organ or the penis. Unfortunately the British Museum specimen does not allow one to give any account of these characters. The funnel organ is too poorly preserved for description. The specimen had already been dissected and no sign of the penis remains ; it was probably small and undeveloped since the animal is not sexually mature. There are no spermatophores.

TABLE III.—Octopus vincenti *n. sp.* *Tabular comparison of specimens.*

Specimen	ML	MWI	HWI	MAI	WDI	SnI	Gill	LLI	CLI	SpLI
Holotype : ♂ (Adam, 1952) .	29	55	59	50*	34	9·5	10	6·2	40	55†
♀ (Adam, 1952) . . .	25	72	60	40*	22	9·0	10	—	—	—
BM.1889.4.24.17, ♂ . .	25	88	68	42	28	8·0	9	5·6	40	—

* Calculated from Adam's index (Longest arm/Mantle length).

† Calculated from Adam's Fig. 53 $D_1 + D_2$. It is not quite clear whether the two sections, horn and sperm reservoir respectively, show the complete spermatophore or whether a middle piece has been omitted. If this is the case the spermatophore length index would be greater.

DIAGNOSIS : A medium-sized species (mantle-length 24–29 mm.) with granular skin and bodily proportions similar to those of immature specimens of *O. vulgaris*. The arms are short, 2 to 2·5 times the length of the mantle, the first arms shortest. The web is deep, about one-third the length of the longest arm, the D sector deepest, the A sector shallowest. The suckers do not exceed 10% of the mantle-length and there are no specially enlarged suckers in either sex. The funnel organ is not known. The gills have 9 or 10 primary lamellae in each demibranch ; the high number resembling that found in *O. vulgaris*. In the male the third right arm is hectocotylized and the ligula represents 4·5–6·2% of its length, the calamus opens near the middle, two-fifths of the distance from the last sucker to the tip of the ligula. The spermatophore is about half the length of the mantle and the horn is straight, without coils. The size of the eggs is unknown.

It may be enquired whether any other specimens, either among those listed by Adam or in the series from the British Museum can reasonably be assigned to this species. British Museum males have the characteristic minute ligula of *O. vulgaris*.

A juvenile male from the Cape Verde Islands (B.M., 1855.9.29.2) can also be excluded. The arms are longer and the web less deep, moreover the state of immaturity at a mantle-length of 31 mm. indicates that it is the young of a large species. The immature female from the Cape Verde Islands (B.M., 1851.1.24.1) with a mantle-length of 50 mm. may be excluded for similar reasons, including also the larger relative size of the suckers. Among Adam's specimens there are two males that have an unusually large ligula for *O. vulgaris* (Goree, 10.vi.1947, LLI 3·5; Goree, 24.ix.1946, LLI 2·9) but the spermatophore of the latter, illustrated by Adam (Fig. 53A), is typical of *O. vulgaris*, with a spirally coiled horn. Moreover in both these specimens the arms are long, the web only of moderate depth, and the suckers large as in *O. vulgaris*. Among females there is one (Goree, 31.i.1950) with unusually short arms, a moderately deep web, and small suckers, that might well be referred to this species. However, the characters of the females present no clear cut distinctions by which one species could be separated from the other. A clarification of the problem must await the capture of a gravid specimen; it may be anticipated that the ripe eggs may show some distinctive features.

It is unlikely that the sexually mature male of *O. vincenti* could be confused with any other Atlantic species. The differences between this species and *O. vulgaris* have already been discussed. In the western Atlantic there are four Caribbean species that have a ligula of approximately the same proportions as in *O. vincenti*. *O. briareus* Robson is readily excluded, the arms are long, the number of gill lamellae low, and the spermatophore horn is coiled. *O. joubini* Robson is a nearly smooth-skinned species with short arms, the spermatophore horn is straight but the number of gill lamellae is low, well below the minimum recorded for *O. vincenti*. The ocellate species, *O. hummelincki* Adam, has, in addition to this distinctive feature, a low number of gill lamellae and a coiled spermatophore horn. The nearest affiliation would appear to be with *O. burryi* (Voss, 1950, 1951). This species has a characteristic color pattern in the form of a purplish band which extends the full length of each arm on the inner (dorsal) side. Apart from this highly distinctive feature, it shows a general resemblance to *O. vincenti* and, in preparing a key for the separation of the two species it would be necessary to depend primarily upon the presence or absence of the purple arm band. Thus the arms are short, the web deep, and the number of gill lamellae high. The ligula is similar in size to that of *O. vincenti* and the horn of the spermatophore is nearly straight with only a few spiral turns (one proximal and three distal in the one that has been described).

The problem of *O. rugosus* in the Indian Ocean is so little understood that it would be futile, at the present time, to offer any comparison with these or other oriental forms.

My best thanks are due to Dr. W. J. Rees for facilities to study the British Museum specimens.

SUMMARY

1. Twenty-two specimens from the eastern Atlantic, the west African coast and South Africa which Robson (1929) identified as *O. rugosus* and which are now in the Collections of the British Museum have been re-examined.

2. Fifteen are either juvenile or sexually immature but, with one doubtful exception, they can reasonably be assigned to *O. vulgaris* Lam.

3. One juvenile specimen from Madeira has a peculiar zebra pattern on the arms and may therefore represent the young of some different species.

4. Six of the 7 adults show no features which would justify their separation from *O. vulgaris* Lam.

5. One adult male from the Cape Verde Islands is assigned to a new species. A male and female of this species were described but not named by Adam (1952) and Adam's male has been designated as the Holotype of *Octopus vincenti* n. sp.

6. The nature of the South African *vulgaris-rugosus* population is discussed and it is concluded that, at most, the South African specimens may represent a local race of slightly smaller size and with other minor differences, not specifically separable from *O. vulgaris* Lam.

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PART II.—A RE-EXAMINATION OF THE SPECIMENS OF *ROBSONELLA FONTANIANA* IN THE COLLECTIONS OF THE BRITISH MUSEUM

Robsonella (= *Joubinia*) *fontaniana* (Orbigny) is a well defined species, endemic to the subantarctic or antiboreal region of South America. Supposed records of this species from the Indian Ocean and from the Central Pacific are subject to the gravest suspicion, as pointed out by Robson (1929). Massy (1925) described a specimen from Natal which Robson has considered to be a local variety. Two closely related but supposedly distinct species have been described from Australia and New Zealand, viz. *R. australis* (Hoyle) and *R. huttoni* Benham. *Polypus campbelli* of Smith is included in the synonymy of *R. australis* (Robson, 1929, footnote p. 145).

Robson (1929) placed *fontaniana* and *australis* (+ *campbelli*) in the new genus *Joubinia* but this was shown to be pre-occupied and the name *Robsonella* was substituted by Adam (1938). The characters of the genus were summarized by Robson and have been reviewed recently by Dell (1952). They are as follows : the arms are subequal, the web is deep and subequal, the mantle aperture is partly closed, the adlateral tooth of the radula is supposedly bicuspid, the penis has a long primary and a small secondary diverticulum, and the ligula of the hectocotylus is remarkably stout with inrolled sides and wide cheeks. We may disregard the characters of the arms and web since these are not of generic value. The partial closure of the mantle is also unimportant since many species of the genus *Octopus* have a slightly narrowed mantle opening of Robson's type B, moreover the mantle aperture is wide in *R. australis* (Benham, 1942). The long diverticulum of the penis is highly distinctive as a species character, common to all three forms, but there are species of *Octopus* which show a similar feature. The secondary diverticulum to which Robson attached great significance is apparently a variable feature since it was lacking in one of Dell's specimens of *R. australis*. There remains only the remarkably stout form of the ligula which may be conveniently retained, at least for the present, as a generic character. However it appears probable that the genus *Robsonella* is not a valid one and that the species which have been assigned to it should be returned to the genus *Octopus*.

A second problem concerns the validity of the distinction between *R. fontaniana* and the two Australasian species. Time did not permit a re-examination of the specimens of *R. australis* (+ *campbelli*) which are in the collections of the British Museum, but the material has been well described and we have also the accounts of Benham (1942) and Dell (1952) for comparison. The entire series of 11 specimens of *R. fontaniana* was carefully re-examined with a view to confirming and enlarging our concept of this South American species (Tables I and II). There are insignificant differences between the mean values of the indices as given by Robson (1929) and as determined here. In addition there are some features which call for further discussion.

TABLE I.—Robsonella fontaniana (*Orbigny*). *Bodily characteristics of eleven specimens in the Collections of the British Museum.**

B.M. No.	Sex	ML	MWI	HWI	MAI	WDI	SnI	SeI	Gill
1851.1.24.5	♂	32	84	75	27	19	11·0	17·2	9·5
1869.6.5.54	♂	24	108	71	34	32	10·2	14·6	9
1869.6.5.65	♂ juv.	19	84	68	28	16	10·5	13·2	*ca.* 8
1869.6.5.69	♂ juv.	19	100	55	35	18	6·8	9·5	10
1851.1.24.12	♀ mat.	24	92	67	39	32	12·5	—	10
1848.6.16.2	♀	35	69	54	32	21	10·0	—	9
1869.6.5.63	♀	27	78	63	34	20	7·4	—	9·5
1868.7.10.2	♀	25	72	68	42	32	11·4	—	10·5
1899.8.31.84	♀	22	96	87	39	25	9·1	—	9
1869.6.5.62	♀	22	104	73	37	30	11·4	—	*ca.* 9
1851.1.24.4	juv.	10	100	90	42	29	10·0	—	10
Average			99	77	37	25	11·0	13·8	9·5

* Symbols as in Pickford (1945).

TABLE II.—Robsonella fontaniana (*Orbigny*). *Characteristics of male specimens in the Collections of the British Museum.**

B.M. No.	LLI	CLI	PLI	SpLI	Sp. Horn	Comments
1851.1.24.5	7·8	50	23·5	165	No coils	—
1869.6.5.54	5·1	50	27	83	One turn	—
1869.6.5.65	(damaged)		18·5	(not formed)		Immature
1869.6.5.69	3·9	56	15·8	(not formed)		Immature

* Symbols as in Pickford (1945).

Robson's sucker-diameter index does not distinguish between the diameter of the largest suckers of the normal series and the diameter of the specially enlarged suckers. It was found that such specially enlarged suckers occur only in males and are present in the four representatives of this sex that were examined. The penis of the two adult males is as figured by Robson, with an accessory knob-like diverticulum. The penes in the two immature specimens are similar but they lack the secondary diverticula. The ligula-length index averages 6·5 in the two adult specimens; as might be expected it is somewhat smaller in an immature male.

Two spermatophores were found in the larger male (B.M., 1851.1.24.5), lodged in Needham's organ, and one was removed for study. It is poorly preserved and doubled upon itself in a knot in the middle region. The estimated length of the horn plus middle piece is 38 mm., the sperm reservoir measures 15 mm. The total length is thus half as long again as the mantle (SpLI 165). The horn is dark and opaque and there is no evidence of coiling. Towards its distal end, i.e. proximal to the knot-like tangle, the inner tube has a moniliform appearance due to a series of three constrictions which are probably artifacts of preservation.

A single spermatophore was found in the smaller male (B.M., 1869.6.5.54). The horn plus middle piece measure 13 mm. and the sperm reservoir measures 7 mm.

The spermatophore-length index is thus lower than in the larger specimen (SpLI 83). The horn is straight except for a single widely-open turn of a spiral towards its distal end.

Nearly all the females are sexually immature with small and relatively undeveloped ovaries. However, the reproductive ducts are well developed and have been described by Robson. It may therefore be inferred that the specimens are spawned out or in a state of sexual quiescence rather than immature. Robson calls attention to the distal portion of the oviduct, or vagina, which is long and stout, but I find that this feature is somewhat variable. One specimen (B.M., 1851.1.24.12) has a well developed ovary with moderately large-sized eggs, *ca.* 3·5 mm. in length. The eggs are not fully ripe and the length of the stalk could not be determined. The vagina of this specimen is not abnormally stout.

DISCUSSION

Table III gives a comparison of indices and numerical characteristics of the species of *Robsonella*, compiled from data presented by Robson (1929), Benham (1942, 1943), and Dell (1952), and from the re-examination of the British Museum series of *R. fontaniana*. This table demonstrates the difficulty of assessing the differences between the three species. *R. huttoni* differs from *R. australis* in its larger size, narrower body and much narrower head but a familiarity with the complexities of octopodan taxonomy suggests that these features are difficult to evaluate. The same is true of the relatively somewhat smaller size of the suckers. Both these Australasian species differ from *R. fontaniana* primarily in the smaller number of gill lamellae ; the ranges, however, overlap and the type of " *campbelli* "

TABLE III.—*Comparison of the species that have been assigned to the genus* Robsonella.*

Species	ML range	MWI av.	HWI av.	ALI av.	WDI av.	SnI av.	SeI‡ av.	Gill range	LLI range
R. fontaniana (Orbigny)									
B.M. Series†	10–35	99	77	(74)	25	11·0	13·8	8–10	5·1–7·8‖
R. australis (Hoyle)									
Robson (1929)									
australis	22–33	81–86	62–73	72–76	33	11–13	—	6–9	10·8
" *campbelli* "	28	85	71	78	28	?	21	10	8·5
Benham (1942)	10–36	79	62	73	24	12	—	6–8	8·4
Dell (1952)	11–30	76	63	73	27	10·6	—	6–8	4·5–4·7
R. huttoni (Benham)									
Dell (1952)	43–56	68	44·5	74	22	9·4	—	6–7	6·6–6·8

* Symbols as in Pickford (1945). Doubtful specimens from the Indian Ocean and Central Pacific excluded.

† Based on new measurements except for the arm-length index which is taken from Robson (1929) and which had to be used, instead of the mantle-arm index, to permit comparison with the published data for the other forms.

‡ Specially enlarged suckers found only in males.

‖ Sexually mature specimens only.

has fully as many lamellae as a typical specimen of *R. fontaniana.* It must be remembered that an accurate count of the number of primary lamellae is highly subjective, depending upon the number of minute terminal foliations that are included in the count. However, the difference appears to be a valid one and must be accepted as such in the present state of our knowledge of these species. As indicated by Dell (1952) *R. huttoni* will probably prove to fall within the range of *R. australis*, but it is also evident that the Australasian specimens are at least racially distinct from the South American form.

A few more points may be discussed. The eggs of *R. australis* measure 2·5 mm. in length and have a short stalk (Benham, 1942). The eggs of *R. huttoni* are of about the same size, 3 mm. (Benham, 1943). Eggs, similar in size, measuring about 3·5 mm., are present in the ovary of a mature female of *R. fontaniana*, described here.

The characters of the hectocotylus and penis have been fully discussed by previous investigators and appear to offer no evidence for separating the species. Attention may be called to a curious error in Dell's paper, in discussing the affinities of *R. huttoni* he states on p. 40 that "The ligula index is appreciably lower than in *australis*—average 6·7 as compared with 10·8." But his table (p. 34, Table 9) shows that his own specimens of *R. australis* have a low index, averaging 5·4. The specimens appear to have been sexually mature since the presence of a spermatophore is mentioned in at least one of them.

The spermatophores of *R. fontaniana* are described for the first time. They are nearly as long as the mantle, or considerably longer. The horn is straight, as far as could be determined, or with a single distal turn, but admittedly the preservation is not good. Benham described and figured the spermatophores of *R. australis.* He states that they measured 40 mm. in length. The mantle-length of the male from which these spermatophores were taken is not given, but even his largest specimen has a mantle-length of only 36 mm. Therefore the spermatophore, like that of *R. fontaniana*, is about as long as or longer than the mantle. In the text Benham states that the "projectile apparatus" consists of a "closely-coiled spring". This would lead one to suppose that the horn of the spermatophore was coiled. However, a study of his figures (Benham, 1942, Figs. 6 and 7) suggests quite otherwise. The horn is apparently straight and what Benham mistook for the coils is clearly, in reality, the internal structure of the lumen which always has this delicate spiral structure, irrespective of whether the horn is straight or coiled (compare with the spermatophores of *O. macropus*, figured by Pickford, 1945, Pl. IV). The spermatophores of *R. huttoni* have not been described.

The author is indebted to Dr. W. J. Rees, for facilities to study these specimens.

SUMMARY

1. Eleven specimens of *Robsonella fontaniana* (Orbigny) in the Collections of the British Museum have been redescribed. The spermatophores, described for the first time are nearly as long as or longer than the mantle ; the horn is straight or with a single spiral turn towards its distal end. The eggs are moderately large, *ca.* 3·5 mm. in length.

2. The status of the genus *Robsonella* is discussed. It is considered probable that the two Australasian species, *R. australis* (Hoyle, 1885) and *R. huttoni* (Benham, 1943) are synonymous but together they form an assemblage that is at least racially distinct from the South American species, *R. fontaniana*. The chief distinguishing characteristic is the lower average number of primary gill lamellae in the Australasian species.

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A REVISION OF THE FAMILY EPICRIIDAE
(ACARINA—MESOSTIGMATA)

G. OWEN EVANS

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Pp. 169–200; *Plates* 1–2; 41 *Text-figures*

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A REVISION OF THE FAMILY EPICRIIDAE

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INTRODUCTION

THE family *Epicriidae* Berl. comprises a small group of Mesostigmatid mites readily distinguished in the adult stage by the polygonal network of bi- or tri-furcate tubercles on the dorsal shield and the absence of an ambulacral apparatus on the first pair of ambulatory appendages. This characteristic ornamentation of the dorsum (" seriebus papillarum fuscarum symmetrice reticulato ") was first described as occurring in *Gamasus reticulatus* Grube, 1859, but unfortunately the original description is inadequate for the recognition of its specific identity. In 1877 Canestrini & Fanzago figured a species for which they proposed the name *Epicrius geometricus*, thereby also erecting the new genus *Epicrius*. Later, Canestrini (1885) added a short description of the species. In the meantime, Haller (1881) had given a definition of *Epicrius* and added two other species to it, *Gamasus mollis* Kramer, 1876 and *Epicrius canestrinii* Haller, 1881. His description and figures of the latter are sufficiently detailed for recognition of the species.

Berlese (1886–87) in "Acari, Myriopoda et Scorpiones hucusque in Italia reperta" re-described and figured *E. geometricus* stating that it was found " in totius Italiae muscis, praecipue in montibus." In the same work *E. canestrinii* is referred to as a variety of *geometricus*. Four other species, *Epicrius corniger* Berl., *Epicrius glaber* Berl., *Epicrius laelaptoides* Berl. and *Epicrius mollis* (Kramer) Berl. were also considered to be congeneric with *E. geometricus*. Later, Berlese (1916*a*) emended his concept of the genus *Epicrius* and transferred *corniger*, *glaber* and *laelaptoides* to the genus *Lasioseius* s. lat., and *mollis* to the genus *Epicriopsis* Berl. Further, in Berlese (1916*b*) *Gamasus mollis* Kramer 1876 non Berl., 1887 was considered to be the nymphal stage of *E. geometricus* which therefore falls into synonymy. Three new species of *Epicrius* were also described in this paper, namely, *E. cirratus*, *E. washingtonianus* and *E. parisiensis*. The latter was made the type of a new subgenus *Diepicrius*.

Absolon (1899) erected the genus *Eugamasus* (preoccupied by *Eugamasus* Berl., 1893) for *Eugamasus cavernarum* Absolon found on the excretory material of bats in a cave in Moravia. There is no doubt that this species is an Epicriid, probably of the genus *Epicrius*. It does not appear to have been found subsequently.

George (1906) re-described three species of *Epicrius* from Lincolnshire. The species he identified as *Epicrius mollis* (Kramer) is *Epicriopsis horridus* (Kramer) and what he believed to be *Epicrius canestrinii* has recently been given the new name *Cornubia georgei* by Turk (1943). The specimens of the third species are in the collections of the British Museum (Natural History) and are correctly determined as *Epicrius geometricus* Can. & Fanz. (= *E. mollis*).

Schweizer (1922) listed two species of the genus *Epicrius* from Switzerland, *E. geometricus* and *Epicrius menzeli* Schweizer, 1922. The specimens of the former were collected from three main regions, namely, " Mittelland," " Jura " and " Alpen". The females described from " Mittelland " and " Alpen " were correctly determined, but the female described and figured from the " Jura " was, as will be shown below, *Epicrius canestrinii* Haller.

Trägårdh (1942) in his revision of the genus *Epicrius* unfortunately deals only with *E. mollis*. This paper is important for the historical account of the genus and the description of the larva and the protonymph of the genotype. In addition, Trägårdh has dealt with the classification of the family *Epicriidae* in several papers on the comparative morphology of the Mesostigmata e.g. Trägårdh 1938, 1946*a* & *b*.

Turk (1943) has also added to our knowledge of the *Epicriidae* in his work on the British species. He erected a new genus, *Berlesiana*, for *Epicrius cirratus* Berl. on the basis of the structure of the sternal region in the female. The genus *Cornubia*, which was also proposed in this paper, was later made a synonym of *Ameroseius* Berl. (Turk, 1953). Two species are included in the genus *Epicrius*, namely, *E. mollis* and *E. geometricus*. His *E. mollis*, however, is *Epicriopsis horridus* (Kramer) and this invalidates the discussion in that paper on the synonymy of *E. mollis* and *E. geometricus*.

The most recent work on the genus *Epicrius* is by Willmann (1953). A new sub-genus, *Epicriella*, was proposed for *Epicrius* (*Epicriella*) *minor* Willm.

The object of the present work is to review our knowledge of the classification of the *Epicriidae* and to re-describe and figure, when possible, the known species. This revision is based on material in the collections of the British Museum (Natural History), the Oudemans Collection at Leiden and Dr. Jos. Schweizer's Collection at

Basle. Dr. G. Lombardini has also kindly undertaken comparisons of specimens of two species with the types in the Berlese Collection at Florence.

CLASSIFICATION

The supra-generic classification used in this paper follows that given by Evans (1955) in which the *Epicriina* was divided into two super-families, the *Epicrioidea* and *Zerconoidea.*

MESOSTIGMATA—EPICRIINA

" Mites with the epigynal portion of the genital plate in the female reduced to a narrow chitinized rim overlapping the genital orifice. Male genital opening situated *in the sternal shield in the region of coxae II and III and closed by two plates, the anterior of which bears a pair of hairs.* Chelicerae dentate in both sexes but *without* spermatophoral process in the male. Pedipalps with five free segments, specialized seta on palptarsus two or three pronged" (Evans, 1955).

Super-family EPICRIOIDEA Evans

Epicrioidea Evans, G. O. Bull. Brit. Mus. (nat. Hist.) 1954, Zool. **2** : 295.

Dorsal shield in both sexes provided with bi- or trifurcate tubercles forming a polygonal network, and a pair of large dorso-lateral protuberances of unknown function. Dorsal setae simple, setose or strongly barbed. Both sexes with jugularia; sternal setae II and/or IV may be situated on a sclerotised shield or on the interscutal membrane. Geniti-ventral shield in the female large, flask-shaped or rectangular. Sterniti-genital shield in the male extending posterior to coxae IV. Gnathosoma with four pairs of ventral setae ; corniculi short, digitiform. Pedipalps with the tibia and tarsus fused dorsally. Specialized seta on palp tarsus three-pronged. Peritreme markedly reduced or absent. Stigmata enclosed in the lateral extension of the dorsal shield. Leg I without ambulacral apparatus. Tarsus I (and sometimes tibia I) with specialized, clubbed sensory setae. Legs II–IV with multilobed pulvillus and two claws.

Family EPICRIIDAE Berl.

Epicriidae Berlese, A. Bull. Soc. ent. Ital. 1885, **17** : 129.

The only family of the *Epicroidea* and therefore with the above characters. The *Epicriidae* consists of two genera which may be distinguished as follows:

1. The majority of the dorsal setae more than 100μ in length, simple or setose. Dorso-lateral protuberances large, conspicuous. Tarsus I with three or more clubbed sensory setae . . . . *Epicrius* Berl.
–. The majority of the dorsal setae less than 60μ in length, stout and strongly barbed (fig. 32). Dorso-lateral protuberance small, inconspicuous. Tarsus I with less than three pairs of clubbed sensory setae . *Berlesiana* Turk

I. Genus *Epicrius* Canestrini & Fanzago

Epicrius Canestrini, G. & Fanzago, F., Atti. Ist. Venet. 1877, (5) **4** pt. 1 : 131.
Eugamasus Absolon, Ph. C. K., Zool. Anz. 1899, **22** : 324.
Parasejus Trägårdh, T. Naturw. Untersuch. des. Sarekgebirges. 1910, **4**, 4 : 432.
Epicrius (*Diepicrius*) Berlese, A., Redia, 1916, **12** : 151.
Epicrius (*Epicriella*) Willmann, C., Sitzber. österr. Akad. Wiss. math-nat. Kl. 1953, **1**, 6 : 474.

Dorsal setae simple or setose; the majority longer than 100μ. Dorso-lateral protuberance large. Geniti-ventral shield flask-shaped. Tarsus I with three or more clubbed setae. Other characters as in the definition of the super-family.

Type : *Epicrius geometricus* Can. & Fanz., 1877, (= *Gamasus mollis* Kramer, 1876).

This genus contains five species which may be considered valid and three species of uncertain status pending the re-examination of the type material. The former may be separated according to the following key to both sexes :

Key to the species of the genus Epicrius *Can. & Fanz.*, 1877

Females.

1. Sternal setae II situated on the interscutal membrane between the jugularia and a shield bearing sternal setae III and IV . . . . *Epicrius minor* Willmann
–. Sternal setae II situated on a well-sclerotised shield with setae III or setae III and IV . . . . 2.
2. Dorsal setae D2 and D4 about one-third the length of setae D3 . . . . . 3.
–. Dorsal setae D2 to D4 approximately equal in length. Sternal setae II to IV on an undivided shield. Interscutal membrane between geniti-ventral and anal shields with seven setae . . . . *Epicrius menzeli* Schweizer
3. Projections of dorsal tubercles with rounded extremities (Pl. 1) . . . . . 4.
–. Projections of dorsal tubercles sharply pointed at their extremities (Pl. 2). Sternal setae II to IV on an undivided shield. Interscutal membrane between geniti-ventral and anal shields with four setae. Anal shield with the usual three setae *Epicrius spinituberculatus* sp. n.
4. The seta posterior to the large dorso-lateral protuberance separated from it by a transverse row of tubercles. Sternal setae II to IV on an undivided shield. The four setae between the genitiventral and anal shields each situated on a platelet[1] *Epicrius canestrinii* Haller
–. The seta posterior to the large dorso-lateral protuberance not separated from it by a row of tubercles. Sternal setae IV (metasternals) separated from shield bearing setae II and III. The pair of setae between the geniti-ventral and anal shields not on platelets . . . . *Epicrius mollis* (Kramer) Berl.

Males.

1. Anal shield completely fused with the dorsal shield. Posterior margin of the sterniti-genital shield strongly convex. With three pairs of setae on the interscutal membrane posterior to the sterniti-genital shield . . *Epicrius mollis* (Kramer) Berl.
–. Anal shield free, or partly fused with the dorsal shield. Posterior margin of the sterniti-genital shield truncated . . . . 2.

---

[1] In some specimens the platelets on one side of the mid-ventral line may be fused so that there are only three platelets between the geniti-ventral and anal shields, (see p. 13).

2. Setae D2 and D4 about one-third the length of setae D3 . . . . 3.
–. Setae D2 to D4 approximately equal in length. Ventri-anal shield with ten pre-anal setae . . . . *Epicrius menzeli* Schweizer
3. Projections of dorsal tubercles rounded at their extremities. Region between the sterniti-genital and anal shields occupied by a large rectangular shield bearing three pairs of setae . . . . *Epicrius canestrinii* Haller
–. Projections of dorsal tubercles sharply pointed. With a ventri-anal bearing three pairs of pre-anal setae . . . . *Epicrius spinituberculatus* sp. n.

Epicrius mollis (Kramer), 1876.

Gamasus mollis Kramer, P. Arch. Naturgesch. 1876, **42** : 82 (fig.) ; Berlese, A., Redia, 1916, **12** : 150. *Epicrius mollis*, Trägårdh, I., Ark. Zool. 1942, **34A** (4) : 3 (fig.).

Epicrius geometricus Canestrini, G. & Fanzago, F. Atti Ist. Venet. 1877, **1** : 60 ; Haller, G. Arch. Naturgesch. 1881, **47** : 190 ; Canestrini, G. Prosp. Acarof. Ital. 1877, (5) **4** : 131 (fig.) ; Berlese, A., *A.M.S.*, Padova, 1886, **30** : 8 (fig.) ; George, C. F., Naturalist, 1906 : 265 (fig.).

The writer follows Berlese (1916) and Trägårdh (1942) in considering *G. mollis* to be the nymphal (deutonymphal!) stage of *E. geometricus*. The two main objections to the acceptance of this synonymy are that Kramer's description and figure are not sufficiently detailed for the specific identity of the species and that the original figure of *mollis* shows only one pair of dorso-lateral protuberances whereas *geometricus* is figured with two pairs. It is probable, however, that Berlese examined the type material of *geometricus* before coming to any decision regarding the synonymy of the species so it is assumed that the original figure of *geometricus* is inaccurate. Berlese (1886) figured *geometricus* with one pair of dorso-lateral protuberances and certainly no Epicriid with two pairs of these structures has been described since Canestrini & Fanzago (1887).

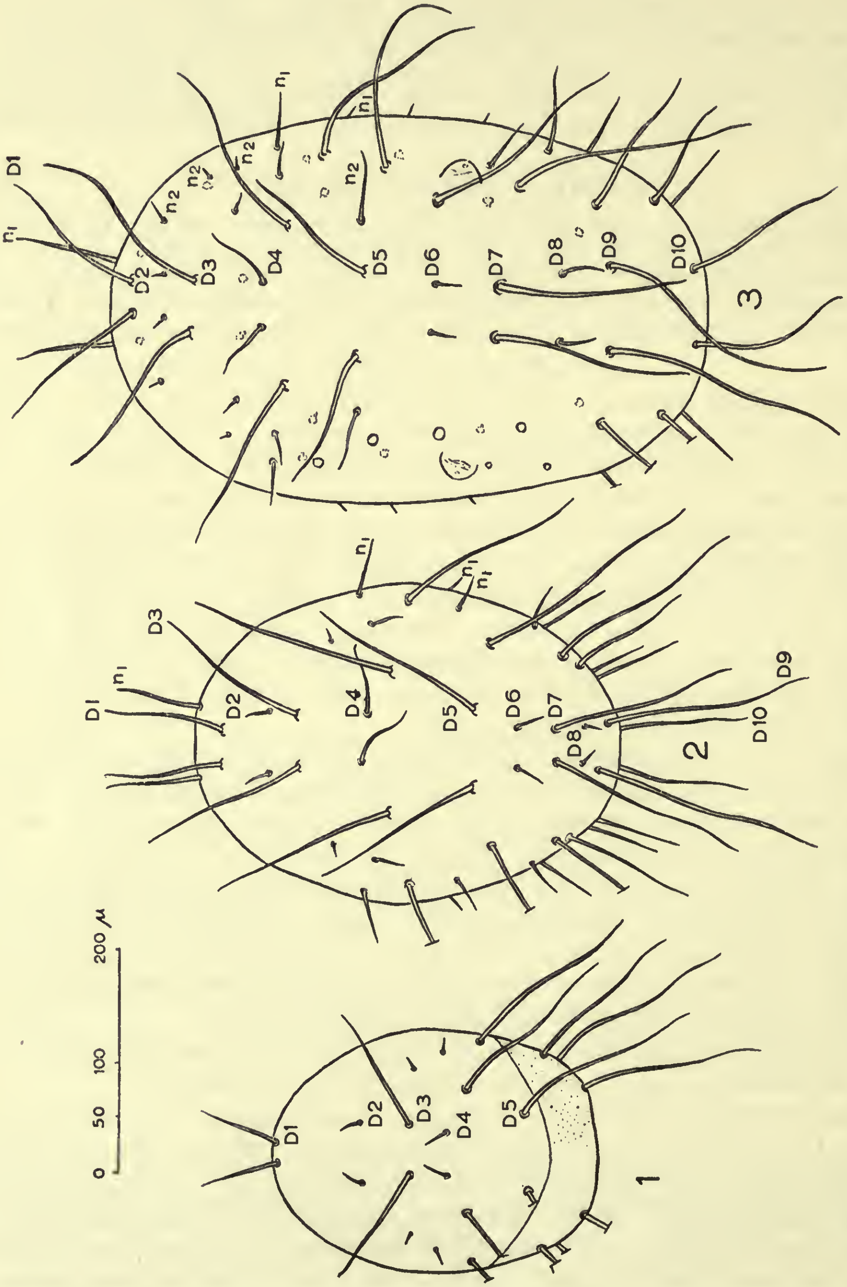
The following re-description of *E. mollis* is based on material collected over a period of twelve months from litter under a Spruce stand in South Bedfordshire.[1]

Dorsal shield. The dorsal surface of the larva is incompletely covered by a weakly sclerotized shield bearing nine pairs of setae distributed as in Text-fig. 1. These setae are probably homologous with those occuring on the anterior shield of the larvae of the free-living Laelaptoidea (Evans, 1953). The interscutal membrane posterior to the shield is granulated and bears three pairs of long whip-like setae. In the protonymph the dorsum is completely covered by a weakly sclerotized shield (Text-fig. 2). The chief features of interest in the chaetotaxy of the shield are :

(1) the addition of five pairs of dorsal setae (D) making a total of ten pairs ; and
(2) the addition of setae n1 in the anterior half of the shield.

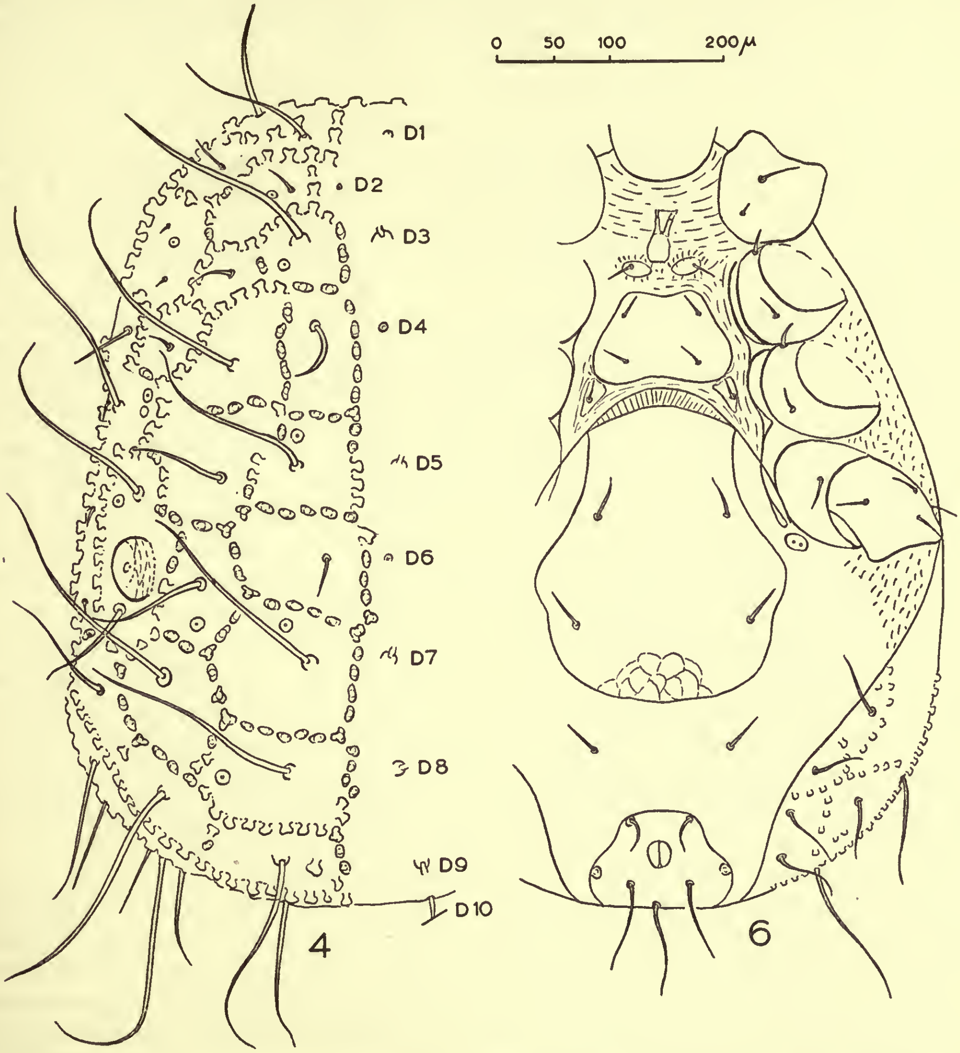
The relative lengths of the setae D1 to D5 are approximately the same in both stages, i.e. D2 and D4 are considerably shorter than D1, and D3. Setae D6 and D7 in the protonymph are much shorter than D7, D9 and D10. The writer has been unable to distinguish, with certainty, between larval and protonymphal setae in the posterior half of the shield. The sclerotized dorsum of the deutonymph is characterized by the development of a pair of large dorso-lateral protuberances (Text-fig. 3).

[1] Collected during investigations financed by H. M. Forestry Commission whilst the writer was on the staff of Rothamsted Experimental Station, Harpenden, Herts.


0
50
100
200 μ
D1
n1
D2
n2
D3
D4
D5
D6
D7
D8
D9
D10
3
2
1

TEXT-FIGS. 1–3. *Epicrius mollis* (Kr.). Chaetotaxy of the dorsum of the larva (Fig. 1), protonymph (Fig. 2) and the deutonymph (Fig. 3). *D*, dorsal series; *n1*, protonymphal setae; *n2*, deutonymphal setae.

The relative lengths of the setae D1 to D10 are approximately the same as in the protonymph. The deutonymphal setae in the anterior half of the shield are indicated by the symbol n2. There is no increase in the number of setae on the dorsal shield from deutonymph to adult (Text-fig. 4). The dorsum of the adult (both sexes) is strongly sclerotized and characteristically ornamented. The ornamentation comprises bi- and trifurcate tubercles forming a polygonal network (Pl. 1). The dorsal setae are setose (Text-fig. 5). The chaetotactic pattern is shown in the figure. Setae D8 which are considerably shorter than D9 in the deutonymph are almost



Text-figs. 4, 6. *Epicrius mollis* (Kr.). Fig. 4, dorsum of female. Fig. 6, venter of female. Abbreviations as Fig. 1.

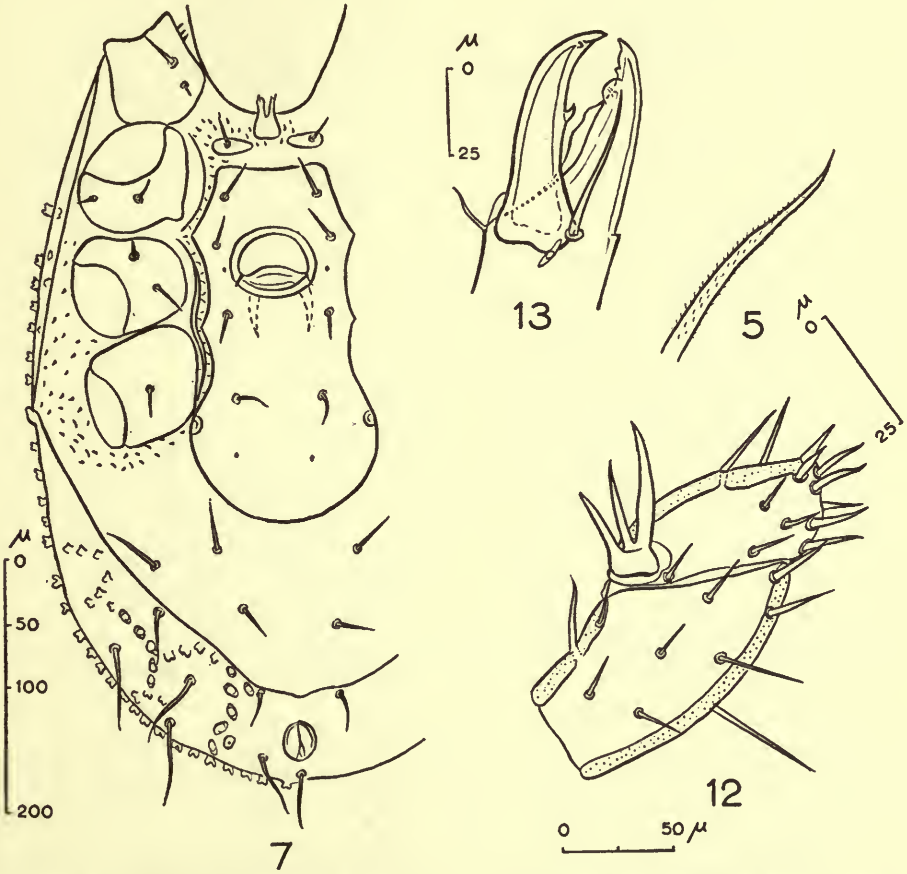
equal in length to them in the adult. The inornate region surrounding the dorso-lateral protuberance carries two setae and a large pore-like structure.

Ventral shields. The ventral surface of the larva is weakly sclerotized. The sternal shield, extending from the posterior margin of coxae I to the posterior margin of coxae III bears three pairs of simple setae. The oval anal shield is provided with a pair of para-anals and a post-anal seta. These setae are long and extend beyond the posterior margin of the body. The interscutal membrane posterior to coxae IV has four pairs of setae of which two pairs are situated between the sternal and anal shields. The sternal and anal region in the protonymph is similar to that in the preceding stage. The region between the sternal and anal shields is provided with three pairs of setae. The sternal shield in the deutonymph bears four pairs of setae and is more strongly sclerotized than in the larva and protonymph. The anal shield has three long setae.

The venter of the female is shown in Text-fig. 6. The first pair of sternal setae are situated on small platelets (jugularia) surrounded by striated membrane. Sternal setae II and III stand on a distinct shield situated between coxae II and III and the metasternals on separate shields postero-lateral to it. The separation of setae IV from the main sternal shield is difficult to detect in specimens not cleared in lactic acid. The sternal shield is not fused with the endopodals. The geniti-ventral shield is large and flask-shaped, and bears two pairs of setae. The epigynal portion of the shield is poorly developed being reduced to a narrow semi-transparent band along the anterior margin of the shield. The region between the geniti-ventral and the ventri-anal shields has a pair of simple setae. The ventri-anal bears a pair of pre-anals and para-anals, and a post-anal seta. The para-anals and the post-anal seta are situated behind the anal opening. There is a pair of conspicuous pore-like structures on the lateral margin of the shield. The remaining sclerotized structures of the venter are a bi-furcate tritosternum, a porose plate situated posterior to coxae IV and the ventro-lateral extension of the dorsal shield, which is provided with a network of tubercles and a number of setae. The interscutal membrane in the region of the jugularia and lateral to the coxae is richly provided with short spines.

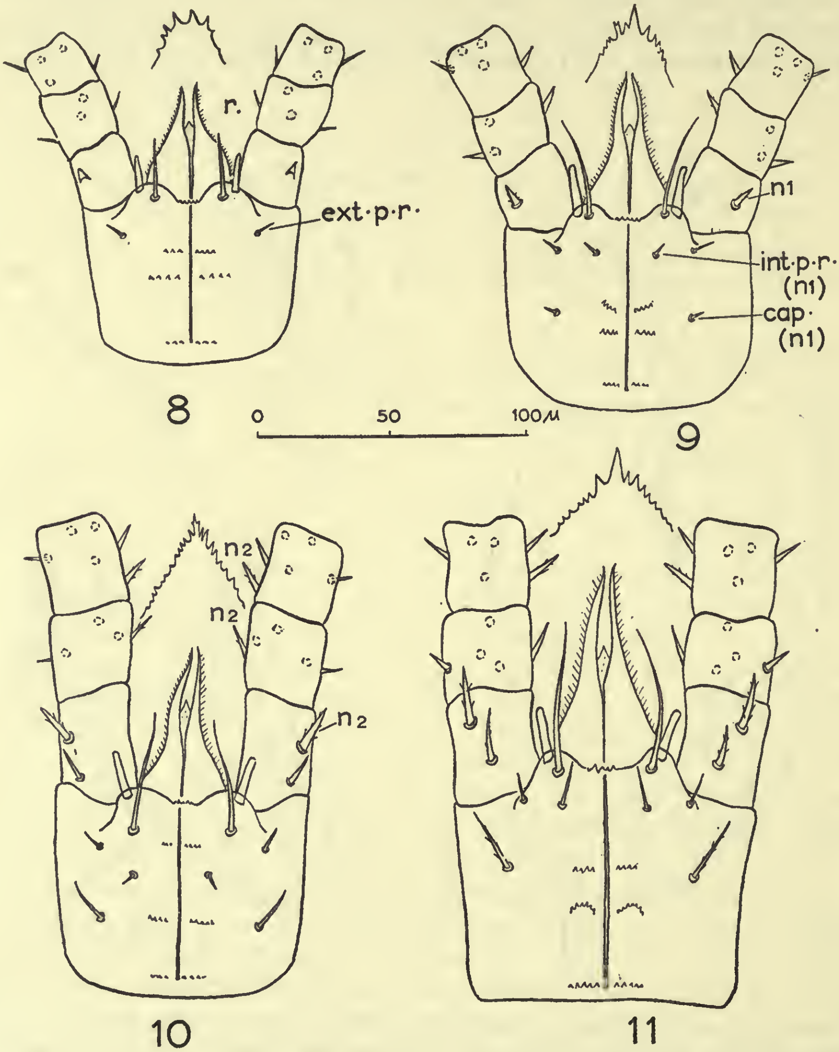
The vental surface of the male differs considerably from that in the female (Text-fig. 7). The jugularia are present in normal position, but the region between coxae II and IV is occupied by a well-sclerotized shield bearing four pairs of setae and three pairs of " pores." This shield, the sterniti-geniti-ventral, extends beyond the posterior margin of coxae IV. It is truncated anteriorly but strongly convex posteriorly. It is not fused with the endopodals. The male genital orifice is situated between coxae III and is covered by two plates. A pair of setae protrude from under the postero-lateral margin of the anterior plate. The ventri-anal shield is fused with dorsal shield, but the setae associated with the anal region are present in the same position as in the female. The interscutal membrane posterior to the sterniti-geniti-ventral shield carries three pairs of setae.

Gnathosoma, pedipalps and chelicerae. The ventral surface of the gnathosoma in the larva is provided with two pairs of setae, namely, the rostrals and the external posterior rostrals (Text-fig. 8). The corniculi are slender and digitiform. There are four rows of denticles in the region of the ventral groove. The pedipalps comprise five free segments. The palptibia and tarsus are divided by a distinct suture ventrally, but are fused dorsally. The specialized seta on the palptarsus is three-pronged. The palptrochanter has a spur-like projection ventro-laterally. The chaetotactic formula for the trochanter, femur and genu is (0–4–5). The ventral surface of the gnathosoma in the protonymph bears two additional pairs of setae—the internal posterior rostrals and the capitular setae (Text-fig. 9). The chaetotactic formula for the palptrochanter, femur and genu is (1–4–5). In the deutonymph there is a further increase in the number of setae on the pedipalp. These additional setae are indicated by the symbol n2 in Text-fig. 10. There is no change in the chaetotaxy of the pedipalp from deutonymph to adult (Text. fig. 11). The structure



TEXT-FIGS. 5, 7, 12, 13. *Epicrius mollis* (Kr.). Fig. 5, distal end of dorsal seta. Fig. 7, venter of male. Fig. 12, palptibia and tarsus (ventral) of female. Fig. 13, chelicera of female.

of the venter of the palptibia and tarsus is shown in Text-fig. 12. These segments are fused dorsally. The development of the chaetotaxy of the gnathosoma and first three free segments of the pedipalp in *Epicrius* is essentially similar to that described by Evans (1953) for the genus *Typhlodromus* Scheuten (*Gamasina—Laelaptoidea*).

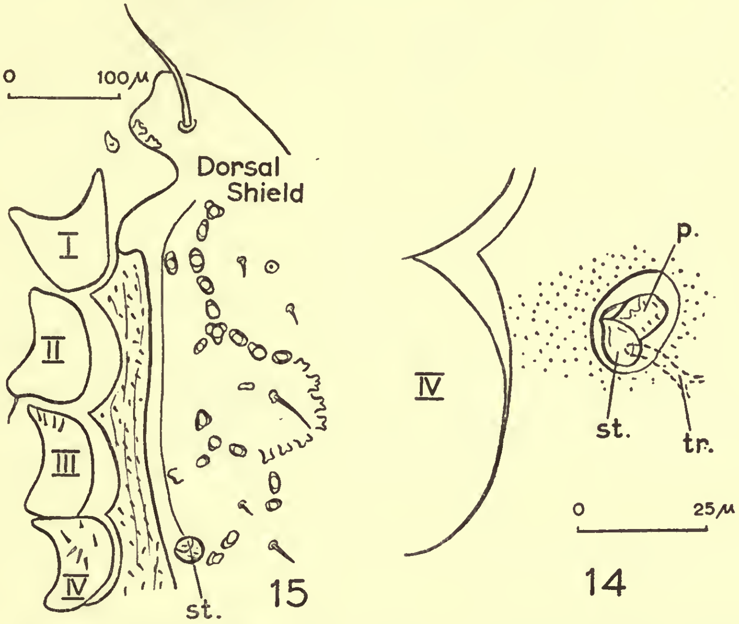


Text-figs. 8, 9, 10, 11. *Epicrius mollis* (Kr.). Gnathosoma (ventral) of larva (Fig. 8), protonymph (Fig. 9), deutonymph (Fig. 10) and female (Fig. 11). *r.*, rostral setae; *ext.p.r.*, external posterior rostral setae; *int.p.r.*, internal posterior rostral setae; *cap.*, capitular setae.

The tectum in all stages is broadly triangular in shape and has a denticulate margin (Text-figs. 8–11). There appears to be considerable variation in the degree of denticulation, at least in the series examined.

The chelicerae are chelate-dentate. The dentition is weak in all stages. The structure of the chelicera of the female is shown in Text-fig. 13.

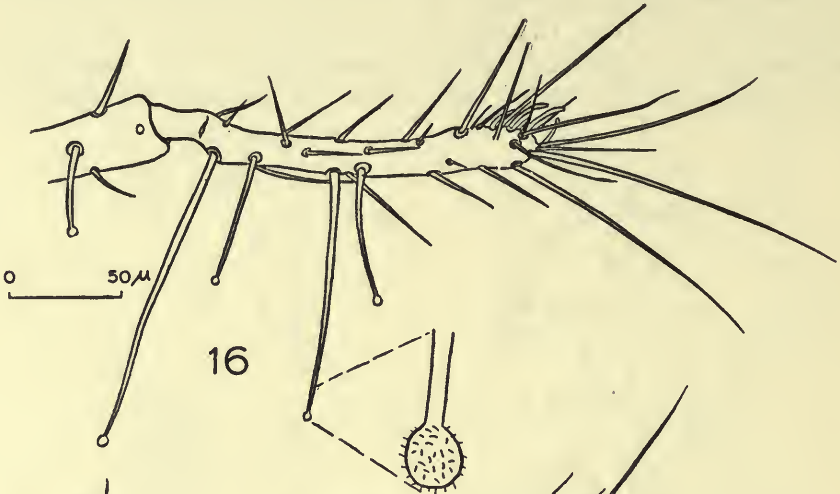
Stigmata and peritremes. The stigmata and peritremes are not developed in the larva. In the protonymph the stigma (*st*) is situated ventro-laterally in the region of the third intercoxal space (Text-fig. 14). The peritreme (*p*) is markedly reduced and is enclosed with the stigma in an oval depression of the body. The main tracheal branch is conspicuous. The stigma and peritreme is the same in the deutonymph.



TEXT-FIGS. 14, 15. *Epicrius mollis* (Kr.). Fig. 14, stigmal region of protonymph. Fig. 15, stigmal region of female. *st.*, stigma ; *p.*, peritreme ; *tr.*, trachea.

In the adult, however, the stigma is enclosed in the heavily sclerotized lateral extension of the dorsal shield. The stigmal opening is situated on a small protuberence (Text-fig. 15). The only indication of a peritrematal plate (?) is the presence of a well-defined line running from the stigma to the level of coxa I and thereby separating a strip of smooth sclerotized plating from the ornamented dorsal shield.

Legs. All the legs comprise six free segments with the terminal segment incompletely separated into a metatarsus and tarsus. Leg I is the longest in all stages and the tarsus is without an ambulacral apparatus. In the adult, tibia and tarsus I are provided with specialized sensory (?) setae ventro-laterally (Text-fig. 16). These long setae, of which there is one on the tibia and four on the tarsus, are club-like distally. The swollen head of the seta is minutely setose. The number and position of these setae are different in the species examined, but since the majority of the specimens were poorly preserved—the distal end of the setae are easily broken off in prepared specimens—full use could not be made of this character. The remaining ambulatory appendages terminate in a multi-lobed pulvillus and two claws (Text-fig. 17). The majority of the setae on the femur to tibia are stout and spinose, and stand on distinct bases.



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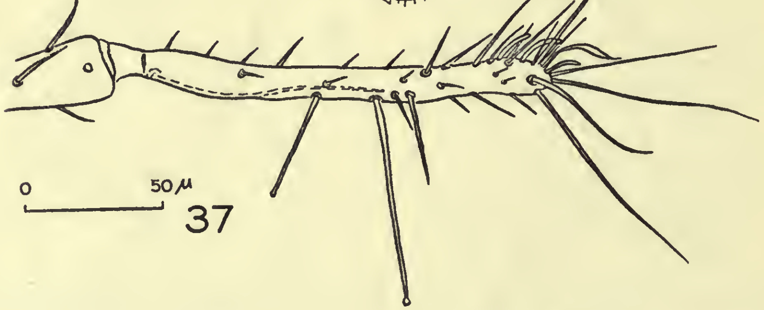

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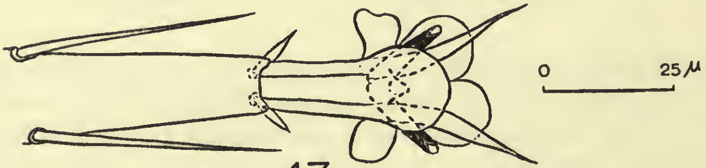

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Text-figs. 16, 17. *Epicrius mollis* (Kr.). Fig. 16, Tibia and tarsus I. Fig. 17, Ambulacral apparatus of Leg. II.
Text-fig. 37. *Berlesiana denticulata* sp. n. Tarsus I.

Dimensions.

Larva, 265–280μ in length and 195–200μ in breadth.
Protonymph, 310–340μ in length and 245–250μ in breadth.
Deutonymph, 440–490μ in length and 305–335μ in breadth.
Female, 640–660μ in length and 405–410μ in breadth.
Male, 570–600μ in length and 360–370μ in breadth.

Locality. This species is the most abundant and widely distributed of the genus. It has been recorded from moss and forest litter in Italy, Austria, Switzerland, Germany, Holland, Sweden and the British Isles.

Epicrius canestrinii Haller, 1881

Epicrius canestrinii Haller, G., Arch. Naturgesch. 1881, **47** : 191 (fig.) ; Oudemans, A. C., Zool. Anz. 1939, **126** : 307.
Epicrius (*Diepicrius*) *parisiensis* Berlese, A., Redia, 1916,[1] **12** : 152, *syn. nov.*
Epicrius geometricus, Schweizer, J. Verh. Natf. Ges. Basel, 1922, **33** : 46 ♀.

The following re-description of *E. canestrinii* is based on specimens of both sexes in the British Museum (Nat. Hist). — from the Michael Collection. The specimens are mounted in Canada Balsam.

Female. The dorsal shield, about 500μ in length and 350μ in breadth, shows the normal network of tubercles. The latter are bi- or trispinate ; the projections having rounded extremities. The dorsal chaetotaxy is shown in Text fig. 18. Setae D2 and D4 are considerably shorter than setae D3, but setae D7, D8 and D9 are approximately equal in length. The dorso-lateral protuberance is well-developed and broadly triangular in shape. The ornamentation in the region of the protuberance differs from that in the other species of the genus examined by the writer. The anterior tubercle seta and the dorso-lateral protuberance are distinctly separated from the posterior tubercle seta by a transverse row of tubercles. The anterior seta is about twice the length of the posterior seta.

Ventrally, the tritosternum and jugularia are normal for the genus (Text-fig. 19). Sternal setae II, III and IV are situated on a rectangular shield extending from the middle of coxae II to the middle of coxae III. The anterior margin of this shield, in the majority of the specimens examined, is concave and the posterior margin convex. The geniti-ventral shield is of the usual form with two pairs of simple setae. The epigynal portion of the shield is well-developed. The interscutal membrane between the geniti-ventral and anal shields bears four pairs of setae. The four setae lying between the geniti-ventral and anal shields each lie on a platelet. The number of platelets appears to be variable. In the female figured by Schweizer (1922) and which the writer has examined, the two platelets on one side are fused. The anal shield is small and provided with three setae, of which the para-anals are situated behind the anal opening.

The gnathosama and pedipalps are normal for the genus. A critical examination of the chelicerae could not be carried out owing to the state of preservation of the specimens.

The legs are also normal for the genus. It was not possible to be certain of the number of clubbed setae on the terminal segments of the first pair of legs. As far as could be seen three clubbed were present on the tarsus.

Male. The ornamentation and chaetotaxy of the dorsal shield is similar to that in the female. The chief differences between the sexes is to be seen in the structure of the ventral surface.

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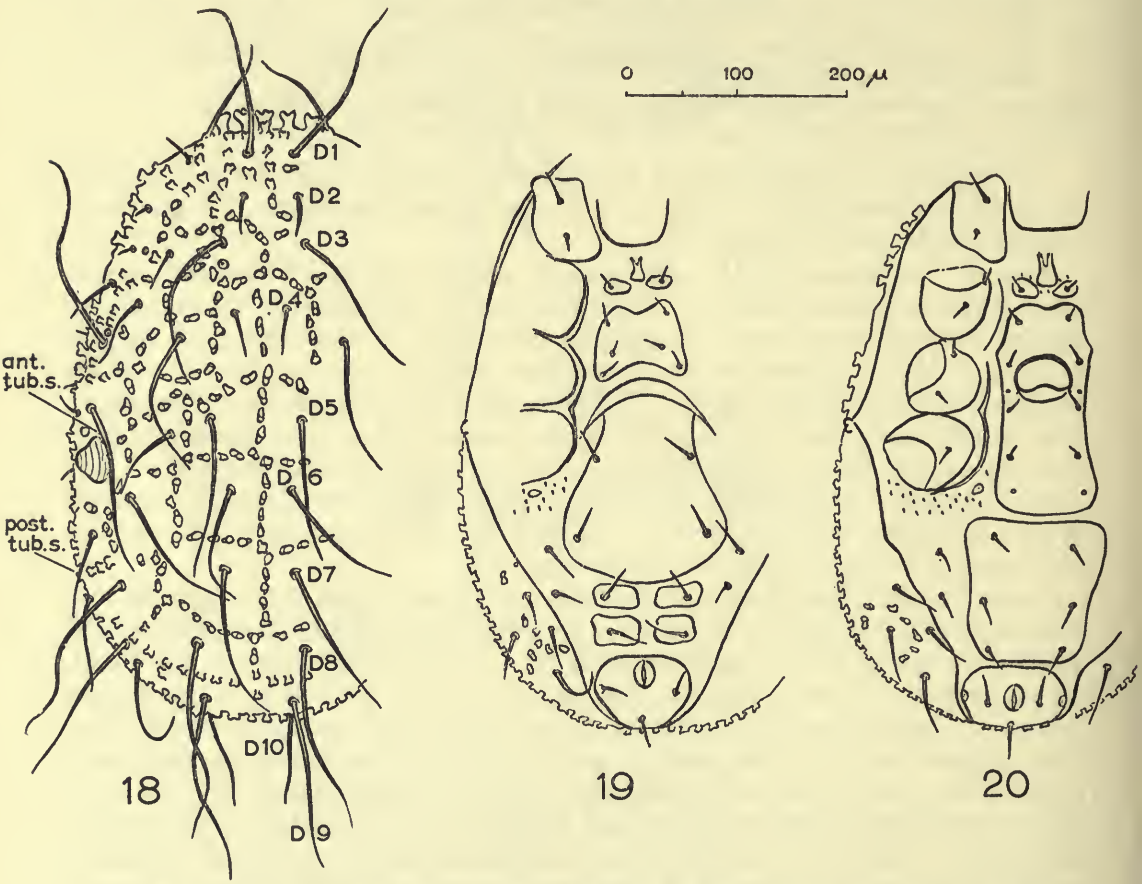
[1] Volume **12** of *Redia* was published on 25.iv.1917, but separates of Berlese's paper containing the description of this species are stated to have been published on 23.viii.1916 (see p. 177).

The elongate sterniti-genital shield, posterior to the paired jugularia, has four pairs of setae and two pairs of " pores." It extends from the middle of coxae II to beyond the posterior margin of coxae IV. The posterior margin of the shield is truncated (Text-fig. 20). The region between the sterniti-genital and anal shields is occupied by large rectangular shield bearing three pairs of setae. Either side of this shield, on the interscutal membrane, are two setae. The anal shield, partly fused with the dorsal shield, is about as broad as long and has three setae and a pair of pore-like structures. The para-anals lie on the level with the posterior margin of the anal opening.

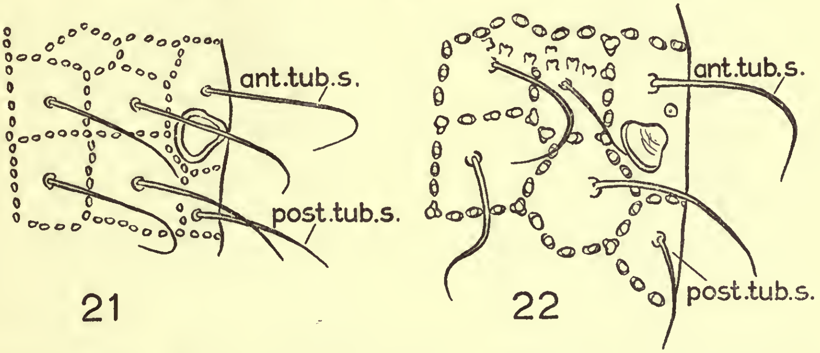


Text-figs. 18, 19, 20. *Epicrius canestrinii* Haller. Fig. 18, dorsum of female. Fig. 19, venter of female. Fig. 20, venter of male. *ant.tub.s.*, anterior tubercle seta; *post. tub.s.*, posterior tubercle seta.

Dimensions. Female : 520–550µ in length, 340–352µ in breadth. Male: 480–520µ in length, 297–320µ in breadth.

Locality. The type locality is in the vicinity of Bern, Switzerland. It occurs in moss and decaying vegetable material and has subsequently been recorded from the following areas: Meudon (nr. Paris), France (Berlese, 1916); Dissenhofen and Jouxtal, Switzerland (Schweizer, 1922); Porth Gwarra, Cornwall, England (Michael Coll.); and Delden, Holland and Sucy-en-Brie, France (Oudemans Coll.).

This species may be readily separated from other species of the genus by the structure and chaetotaxy of the region of the dorso-lateral protuberance. Haller (1881), in his original description of the species, deals only with the structure of the dorsum. He gives a figure of dorso-lateral protuberance and associated setae showing the separation of the posterior tubercle seta from the tubercle (Text-fig. 21). This figure agrees very well with the one based on material examined by the writer (Text. fig. 22).



Text-figs. 21, 22. *Epicrius canestrinii* Haller. Ornamentation and chaetotaxy in the region of the dorso-lateral protuberance of the female. Fig. 21, after Haller (1881). Fig. 22, specimen in the Michael Collection. Abbreviations as in Fig. 18.

The male of *Epicrius* (*Diepicrius*) *parisiensis* Berlese agrees in all details with the male of *E. canestrinii.*

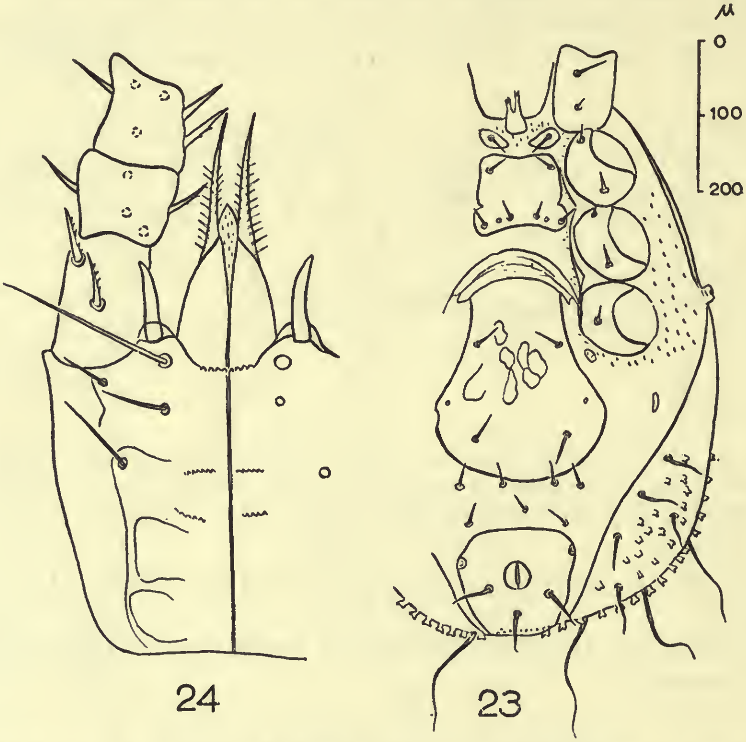
Epicrius menzeli Schweizer, 1922.

Epicrius menzeli Schweizer, J. Verh. Natf. Ges. Basel, 1922, **33**: 47, figs. ♂ & ♀.

The following re-description of *E. menzeli* is based on the type material kindly lent to the writer by Dr. J. Schweizer, Birsfelden.

Female. The dorsal shield, $748\mu \times 451\mu$, is provided with a network of tubercles as in other species of the genus. The tubercles are bi- and trispinate. The setae of row D are considerably more uniform in length than in the preceding species—setae D2 and D4 being approximately equal in length to D3. The dorso-lateral protuberance is strongly formed and the setae lying immediately anterior and posterior to it are contained in the same area.

Ventrally, the tritosternum is normal for the genus (Text-fig. 23). The first pair of sternal setae are situated on distinct platelets. The remainder of the sternal setae lie on a large sternal shield extending from the middle of coxae II to the middle of coxae III. Sternal setae II are widely separated from setae III and IV, which lie in a transverse line along the posterior margin of the shield. A pair of distinct " pores " lies between setae III and IV. The geniti-ventral shield is large and flask-shaped, with two pairs of setae. The epigynal portion of the shield extends a considerable distance beyond the genital orifice. The geniti-ventral is faintly sculptured and has a pair of " pores." The interscutal membrane between the geniti-ventral and the anal shields bears seven setae arranged as in the figure. The anal shield has three setae and a pair of large pore-like structures (muscle attachments (?)). The para-anal setae are situated posterior to the anal opening. The metapodalia are small, as are the porose-plates posterior to coxae IV.

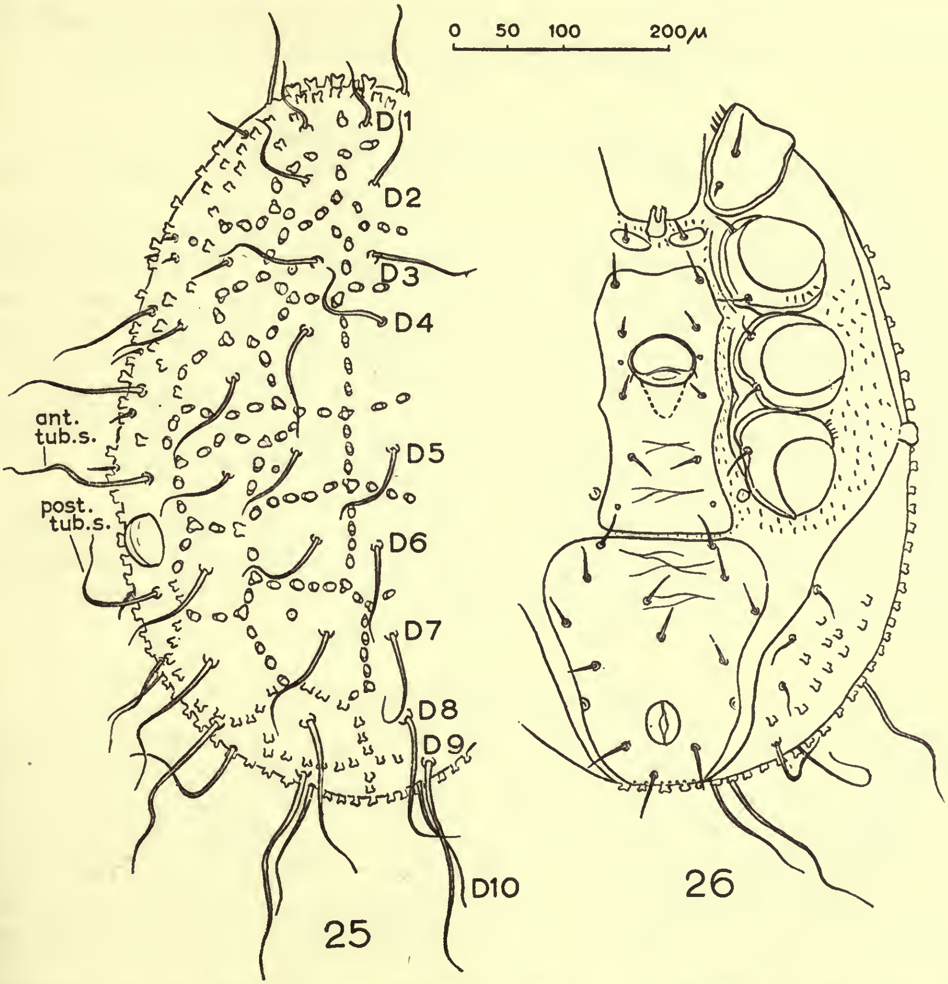


TEXT-FIGS. 23, 24. *Epicrius menzeli* Schweizer, female. Fig. 24, gnathosoma (ventral). Fig. 23, venter.

The gnathosoma and pedipalps are normal for the genus (Text-fig. 24). The rostrals (240μ), the interior posterior rostrals (77μ), the exterior posterior rostrals (66μ) and the capitular setae (110μ) are distributed as in the figure. The chelicerae are chelate-dentate and normal for the genus. The legs conform in general with those in the preceding species. Tibia I (approximately 185μ in length) is provided with one clubbed seta and tarsus I (approximately 220μ) with three clubbed setae.

MALE. The dorsal shield in this sex measures 627–638μ in length and 418–429μ in breadth. The ornamentation and chaetotaxy is basically the same as in the female (Text-fig. 25).

Ventrally, the jugularia are well-developed and widely separated from the sterniti-genital shield (Text-fig. 26). The latter has four pairs of simple setae and two pairs of " pores " distributed as in the figure. The shield is incised anteriorly and truncate posteriorly. It is faintly sculptured. The genital orifice is situated between coxae III. The genital sclerites are as in other species of the genus. The region posterior to the sterniti-genital is occupied by a large ventri-anal shield bearing thirteen simple setae and a pair of conspicuous " pores ". The para-anal setae lie posterior to the anal opening. The shield is faintly sculptured. The porose platelets are situated postero-lateral to coxae IV. The metapodalia are apparently absent.



TEXT-FIGS. 25, 26. *Epicrius menzeli* Schweizer, male. Fig. 25, dorsum. Fig. 26, venter.

The gnathosoma and pedipalps are essentially the same as in the female. The chelicerae were not fully visible in the preparations examined.

Tibia I (176–181μ in length) is provided with one clubbed seta and tarsus I (178–198μ in length) with three clubbed setae.

DIMENSIONS. Female: 748μ in length, 451μ in breadth. Male: 627–638μ in length, 418–429μ in breadth.

LOCALITY. The type material comprises one female and three males collected in damp Beech leaves in a ditch near Bennwil (" Basler Jura "), Switzerland.

Epicrius minor Willmann, 1953

Epicrius (*Epicriella*) *minor* Willmann, C., Sitzber. österr. Akad. Wiss. math-nat. Kl. 1953, **1**, 6 : 474, fig. ♀.

This species is characterized by the structure of the sternal region of the female, the only sex known. Sternal setae II lie on the interscutal membrane between the jugularia and an elongate shield bearing setae III and IV. The geniti-ventral shield is large and flask-shaped with two pairs of setae and a pair of " pores ". The interscutal membrane between the geniti-ventral and the anal shields has one pair of setae only. The anal shield bears five setae, of which the paired para-anals are situated behind the anal opening. The details of the ornamentation and chaetotaxy of the dorsal shield are not given in the original description of the species.

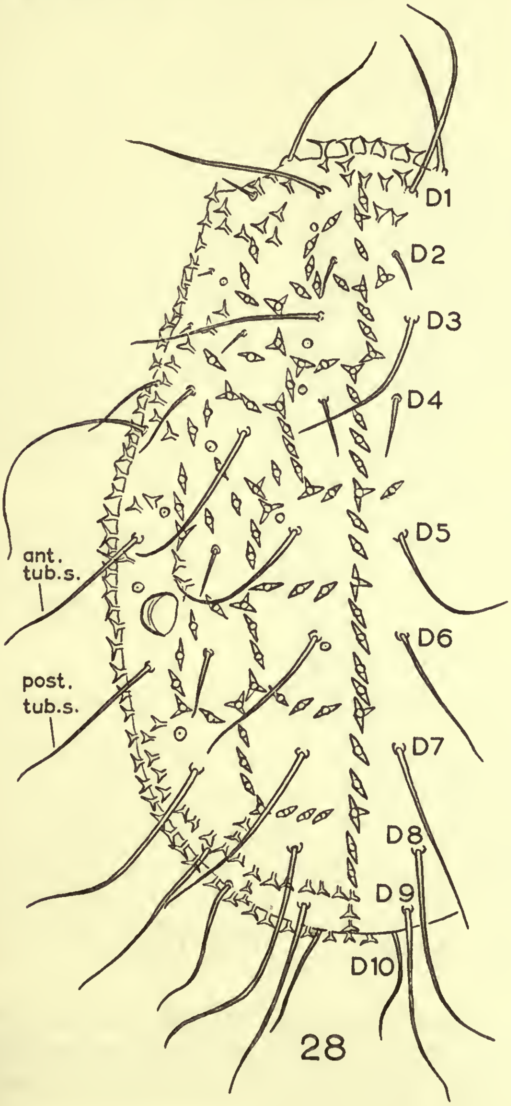
DIMENSIONS. Female 405μ in length, 255μ in breadth.

LOCALITY. " Gipel des Unterberges, etwa 1,300 m., in den Voralpen von Niederösterreich, Waldquadrat in niederem Buchenkrummholz mit zwischenstehenden jungen Fichten . . . Untervegetation bedeckt den Boden zu einem Drittel, viel Buchenfallaub. 11.vi.1939, 1 ♀" (Willmann, 1953).

Epicrius spinituberculatus sp. n.

FEMALE. The dorsal shield, 594μ in length and 396μ in breadth, is richly provided with tubercles forming a distinct network. The structure of the tubercles is unique amongst the genus *Epicrius* in that the distal projections are sharply pointed and not obtuse as in the other species (Text-fig. 27 and Pl. II). The number of dorsal setae is normal for the genus. Setae D2 and D4 are considerably shorter than D3, whilst D7, D8 and D9 are approximately equal in length (Text-fig. 28). The dorso-lateral protuberance is well-developed and the setae lying anterior and posterior to it are contained in the same area.

Ventrally, the tritosternum is normal for the genus (Text-fig. 29). The first pair of sternal setae are situated on distinct platelets, whilst sternal setae II to IV are on a sclerotized shield extending from the middle of coxae II to the middle of coxae III. The distribution of setae II to IV is similar to that in *E. menzeli*. The geniti-ventral shield is flask-shaped, being constricted in the region of the anterior of two pairs of setae which are situated on it. The epigynal portion of the shield is similar to that in *E. mollis*. The striated interscutal membrane between the geniti-ventral and anal shields is provided with two pairs of simple setae. The anal shield is not fused with the dorsal shield and bears three setae. The para-anals are situated behind the anal opening. A pair of large pore-like structures is present antero-laterally on the anal shield. The metapodalia and porose plates are present in the positions shown in the figure.


D1
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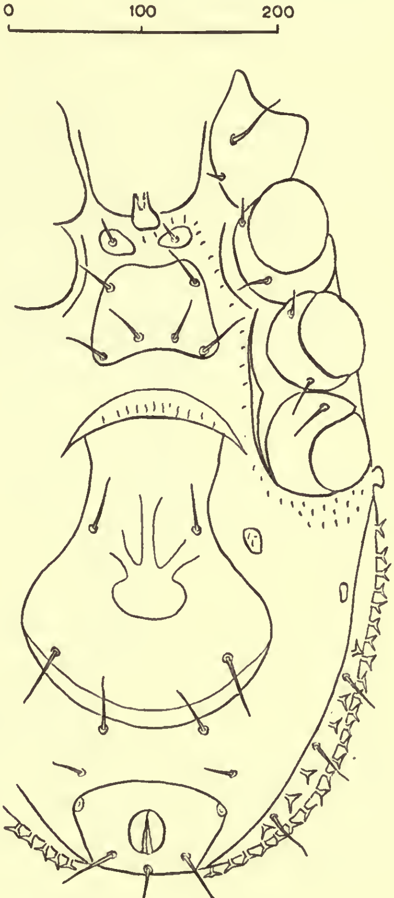

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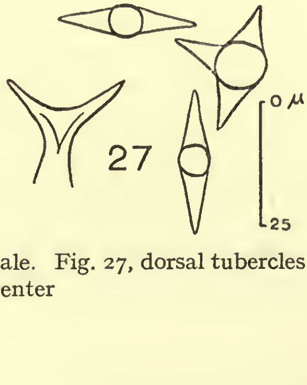

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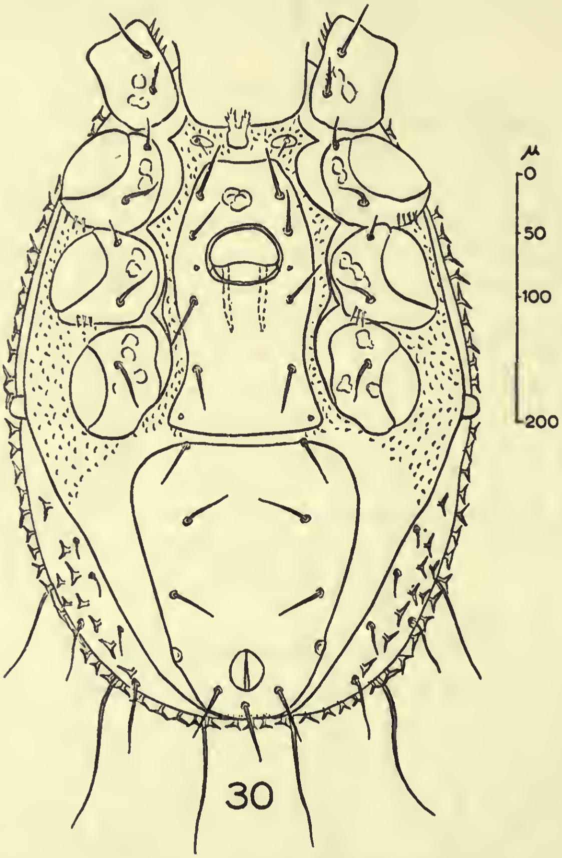
TEXT-FIGS. 27, 28, 29. *Epicrius spinituberculatus* sp. n., female. Fig. 27, dorsal tubercles. Fig. 28, dorsal shield. Fig. 29, venter

The gnathosoma and pedipalps are normal for the genus. The chelate-dentate chelicerae were not sufficiently exposed for critical study.

The general structure of the legs is normal for the genus. Tibia I, 187μ in length, has one clubbed seta. The number of clubbed setae on tarsus I, which is approximately equal in length to tibia I, could not be ascertained owing to the state of preservation of the specimen.



Text-Fig. 30. *Epicrius spinituberculatus* sp. n. Venter of male.

Male. The network of tubercles and the relative length of setae D2–D4 on the dorsum of the male are the same as in the female. The lateral and postero-lateral setae appear to be relatively longer in length, but this may be due to the distortion of the dorsal setae in the female as the result of mounting.

Ventrally, the tritosternum and jugularia are normal for the genus. The sternitigenital shield bears four pairs of simple setae and two pairs of "pores" (Text-fig. 30). The genital orifice is situated between coxae III. The region posterior to coxae IV is occupied by a large ventri-anal shield similar in shape to that in *E. menzeli*, but having only three pairs of pre-anal setae. The para-anals are situated posterior to the anal opening. A pair of large pore-like structures is also present on the shield. The interscutal membrane in the region of the coxae is richly provided with minute spines.

The gnathosoma and pedipalps are normal for the genus. The chelicerae are chelate-dentate.

Tibia I, 154μ in length, is provided with one clubbed seta and tarsus I, 165μ in length, has three of the four macro-setae clubbed.

DIMENSIONS: Female: 597μ in length, 396μ in breadth. Male: 535–540μ in length, 340μ in breadth.

LOCALITY: A single female (holotype, 1930.8.25.2198) labelled *Epicrius canestrinii* Haller in the Michael Collection in the British Museum (Nat. Hist.) The specimen is without a precise locality, as are the majority of Michaels' specimens. Also two males (Allotype, 1954.9.8.2 and Paratype 1954.9.8.3), collected by the writer from a thick layer of humus (F-layer) under bracken in the Leri Valley, near Dol-y-bont, Cardiganshire, Wales, on 19.iv.1954.

E. spinituberculatus may be readily separated from other species of the genus by the structure of the dorsal tubercles, the chaetotactic pattern of the dorsal shield, and the chaetotaxy of interscutal membrane between the geniti-ventral and anal shields in the female.

Species Dubiae

The following three species which probably belong to the genus *Epicrius*, have not been examined by the writer; the descriptions are inadequate for their certain recognition.

Gamasus reticulatus Grube, 1859

Gamasus reticulatus, Grube, A. E., Arch. Naturk. Liv. Ehst.-u. Kurl. 1895, (2) **1** : 459 and 474.
Epicrius reticulatus, Oudemans, A. C., Zool. Anz. 1939, **126** : 306.

The original description is sufficient only to indicate that this species probably belongs to the genus *Epicrius*. The ornamentation of the dorsal shield of the unique specimen is described as " seriebus papillarum fucarum symmetrice reticulato ". The first pair of legs are without claws. The type locality is in Latvia. Grube's material may be in Dorpat or Breslau (Oudemans, 1939).

Eugamasus cavernarum Absolon, 1899

Eugamasus cavernarum, Absolon, Ph. C. K., Zool. Anz. 1899, **22** : 324.
Epicrius cavernarum, Oudemans, A. C., Zool. Anz. 1939, **126** : 307.

The description of this species is chiefly based on the male. The ventral surface in this sex is said to be divided into a number of plates. The sternal plate is small (or narrow) and rounded off, whilst the genital plate, connected with the anal plate behind, is prolonged and rounded off anteriorly. Further the " abdominalplatte " is divided into two distinct plates. The remainder of the description deals with structures which are characteristic of all other species of the genus. The description of the female is too short to be of value in defining the species.

If Absolon's description of the ventral surface of the male is correct, then *E. cavernarum* is undoubtedly a valid species. The writer is inclined, however, to treat it as a *species dubia* until the type material can be re-examined.

E. cavernarum was found on the excreta of bats in a cave (Slouperhöle) in Moravia, Czechoslovakia.

Epicrius washingtonianus Berlese, 1916

Epicrius washingtonianus Berlese, A., Redia. 1916, **12** : 151.

Berlese opens his description of this species by stating that " species hanc describere bene non possum . . . ". The description deals with the ornamentation and chaetotaxy of the dorsal shield only and is as follows :

> "... Tamen a caeteris hucusque notis est diversum, quod corniculis dorsolateralibus (ad quartos pedes) caret et areolis minus numerosis quam in E. cirrato gaudet. Pili dorsi (qui adhuc persistunt) breves, nulla barbula ornati, simplices, forsitan omnes intersese statura subaequales (ad 80μ long.). Tuberculi dorsi plerumque bilobi, rarius trilobi. Ad 600μ long. ; 420μ. lat. Caeteris hucusque notis specibus maior.
>
> Habitat. Inveni in muscis ad ' Washington ' collectis."

II Genus **Berlesiana** Turk, 1943

Berlesiana Turk, F. A., Ann. Mag. nat. Hist. 1943, (11), **10** : 855.

This genus was proposed by Turk for *Epicrius cirratus* Berlese. He considered the structure of the sternal region in that species to be so distinctive that " when the types are re-examined a new family will have to be made ". This would appear to be likely in the light of Trägårdh's concept of the family *Epicriidae* (Trägårdh, 1939). The discovery of a new species undoubtedly congeneric with *E. cirratus* but with sternal setae II and III in the female on an undivided shield shows that the structure of the sternum in the *Epicriidae* is more variable than Trägårdh realised, and cannot be used as a major character in the classification of the *Epicriina.*

The ornamentation of the dorsal shield and the structure of the dorsal setae in *E. cirratus* separates it from the *mollis*—group of species. The writer proposes to retain *Berlesiana* Turk as a valid genus but at the same time emending the original definition as follows :

> With the general characters of the genus *Epicrius* but differing from it in the following characters : tubercles of the dorsum more numerous ; posterolateral protuberance poorly developed ; dorsal setae short, stout and strongly barbed ; geniti-ventral shield in the female more or less parallel-sided ; tarsus I with less than three pairs of clubbed setae.

Type : *Epicrius cirratus* Berl., 1916.

The genus *Berlesiana* contains two species which may be separated by the structure of the sternal shield in female, as follows :

1. Sternal setae II to IV each situated on a separate shield *Berlesiana cirrata* (Berl.)
–. Sternal setae II and III on an undivided shield . . *Berlesiana denticulata* sp. n.

Berlesiana cirrata (Berl.), 1916

Epicrius cirratus Berlese, A., Redia. 1916, **12** : 151.
Berlesiana cirratus Turk, F. A., Ann. Mag. nat. Hist. 1943, (11) **10** : 855.

In the original description of this species Berlese mentions the ornamentation and chaetotaxy of the dorsal shield. The dorsal setae are about 50μ in length. The dorso-lateral protuberance is stated to be absent, but it is possible that Berlese may have overlooked it, since a poorly developed protuberance is present in the normal position in the species described below.

The sternal plate in the female is described as " in partes duas laterales fracto ; quaeque pars autem fissura transversa plus minusve bene in scutulis duobus rotundis, in medio piliferis divisa ". The ventri-anal shield is provided with five setae in the female. The male is not described.

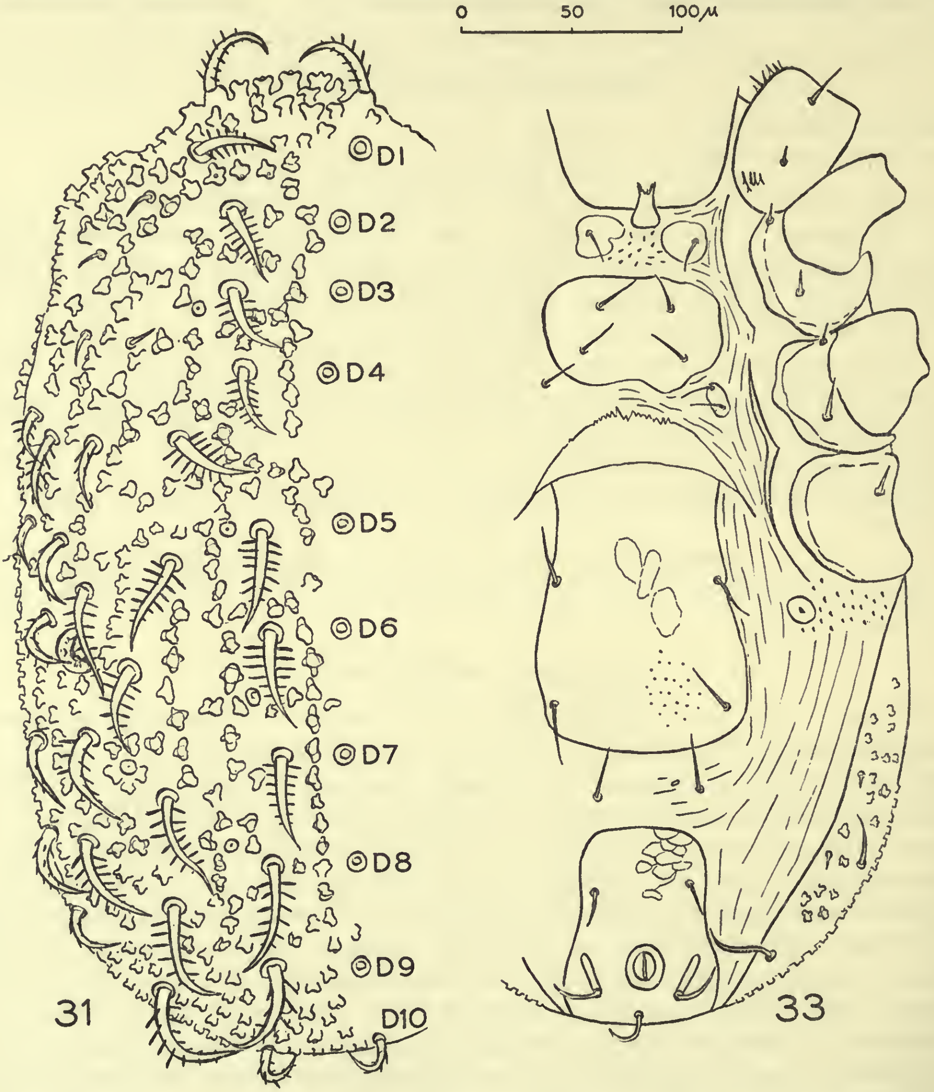
DIMENSIONS. Female : 440μ in length, 300μ in breadth. Male : " considerably smaller ".

LOCALITY. This species is known from the type localities only ; the female from Chianti and Pontedera, and the male from near Genoa. In all localities the species was found in moss.

Berlesiana denticulata sp. n.

FEMALE. The dorsal shield, 415–425μ in length and 260–265μ in breadth, completely covers the dorsum of the mite. The ornamentation of the shield consists of numerous tubercles, predominantly tri-lobed (Text-fig. 31). The dorso-lateral protuberance is not nearly as well developed as in the genus *Epicrius*. The dorsal setae with the exception of four pairs of simple setae antero-laterally, are short (44–55μ), stout and strongly barbed (Text-fig. 32). Setae D1 to D10 are approximately equal in length. The distribution of " pores " is shown in the figure.

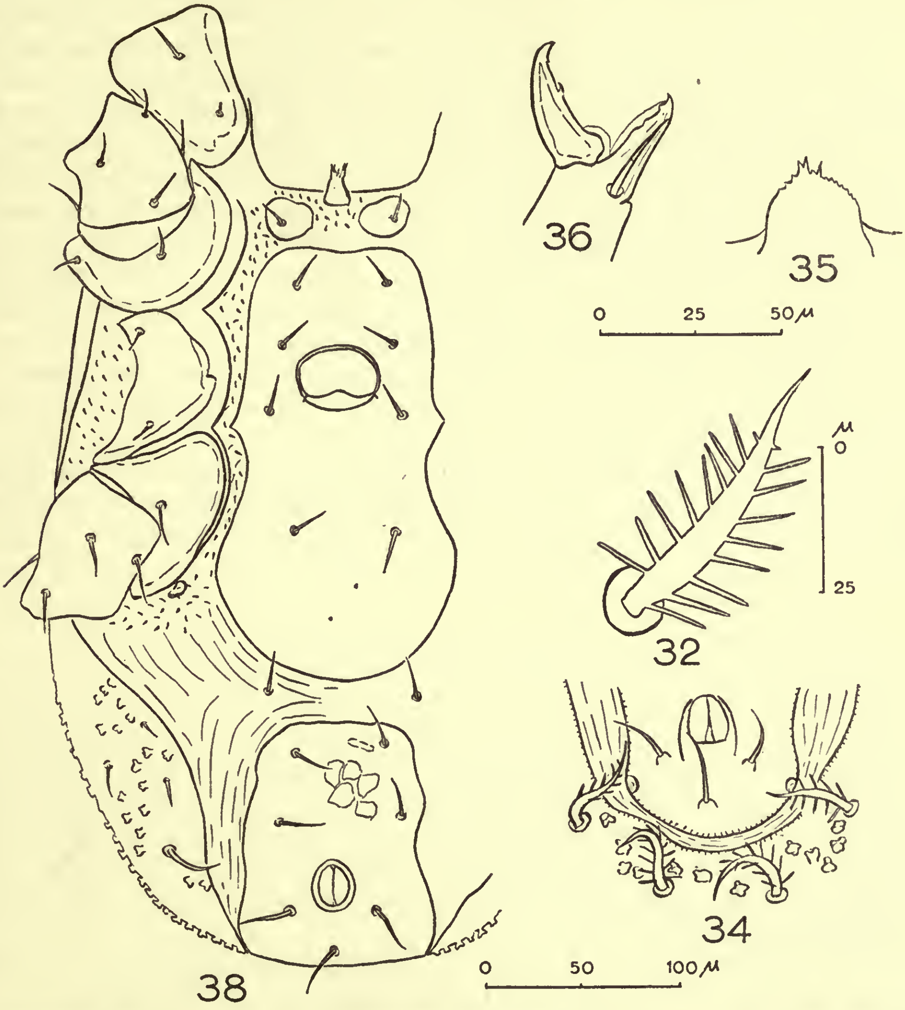
Ventrally, the tritosternum and jugularia are as in the genus *Epicrius*. Sternal setae II and III are situated on an undivided shield extending from the middle of coxae II to the middle of coxae III (Text-fig. 33). Setae IV (the metasternals) lie off this shield. In the holotype the metasternal seta on one side lies on the inter-scutal membrane but on the other side there are two setae situated on a small shield. This is undoubtedly an aberration since in the paratypes sternal setae IV are situated on the interscutal membrane postero-lateral to the shield bearing setae II and III. The geniti-ventral shield is ornamented with punctations and is roughly rectangular in shape. Its posterior margin is truncated. The epigynal portion of the shield is well-developed and denticulate along its anterior margin. The geniti-ventral bears two pairs of simple setae. The endo-podal plates are poorly developed and not fused with the sternal shield. The ventri-anal shield is elongate, truncate anteriorly and provided with a pair of pre-anal setae. The surface of the shield is scabrid. There is a tendency for increased setation of the ventri-anal. In one of the paratypes there are four pre-anal setae. The ventri-anal is not fused with the dorsal shield



Text-figs. 31, 33. *Berlesiana denticulata* n. sp., female. Fig. 31, dorsal shield. Fig. 33, venter.

(Text-fig. 34). A pair of simple setae is present between the geniti-ventral and anal shields.

The gnathosoma is provided with four pairs of setae ventrally of which the rostrals are considerably longer than the other three pairs. The pedipalps have five free segments. The chaetotaxy of the palptrochanter, femur and genu is (2–5–6). The palptarsus is incompletely separated from the tibia; the two segments being fused dorsally. The specialized seta on the palptarsus is three-pronged. The tectum is denticulate and basically the same as in species of *Epicrius* (Text-fig. 35). The chelicerae are chelate-dentate (Text-fig. 36).



Text-figs. 32, 34, 35, 36, 38. *Berlesiana denticulata* n. sp. Fig. 32, dorsal seta of female. Fig. 34, postero-ventral region of female. Fig. 35, tectum of female. Fig. 36, chelicera of female. Fig. 38, venter of male.

Leg I is considerably longer than the body and is without an ambulacral apparatus. Tibia I, about 110μ in length, has no clubbed setae. The chaetotaxy of tarsus I is shown in Text-fig. 37 (p. 182). This segment has two clubbed setae and, proximally a long stout seta lying parallel to the longitudinal axis of the segment. Legs II to IV terminate in a pulvillus and two claws, and are of the form in the genus *Epicrius*.

MALE. The ornamentation and chaetotaxy of the dorsal shield in the male is essentially similar to that of the female.

Ventrally, the jugularia are relatively large and are distinct from the sterniti-genital shield which extends from the middle of coxae II to well beyond the posterior margin of coxae IV. This compound shield bears four pairs of simple setae distributed as in Text-fig. 38. The genital orifice is situated between coxae III and its structure is normal for the family. The surface of the shield appears to be corrugated in preserved specimens. It is not strongly sclerotized. The ventri-anal shield is similar in form to that in the female except that it bears an additional pair of pre-anal setae. The striated interscutal membrane between the sterniti-genital has a pair of simple setae. There is also evidence of increased setation of the ventral shields in the male. In one specimen two short setae were present posterior to the last pair of " sternal " setae on the sterniti-genital.

The gnathosoma, pedipalps and legs are basically the same as in the female.

DIMENSIONS. Female : 415–425μ in length, 260–265μ in breadth. Male : 400–405μ in length, 240–250μ in breadth.

LOCALITY. Five females and seven males from litter under Beech at Boxhill, Surrey (collected by Messrs. S. K. Eltringham and K. H. Hyatt, 21.viii.1953). Holotype female, 1954.9.8.9; Allotype male, 1954.9.8.10; Paratypes, 1954.9.8.11–20.

GEOGRAPHICAL DISTRIBUTION OF THE EPICRIIDAE

Any discussion on the zoogeography of the free-living Acarina is open to criticism on the basis that very little work has been done on them outside the Palaearctic and Nearctic Regions. It is, therefore, not possible to be dogmatic about the limits of distribution of any group of free-living mites. Bearing this in mind, it can be stated that, at present, the *Epicriidae* are recorded only from the Palaearctic and Nearctic Regions ; ten " species " from the former and only one species from the latter.[1] *Epicrius mollis* (Kr.) appears to be the most widely distributed species in the Palaearctic Region having been recorded from a number of localities between Sicily in the south and Sweden in the north.

The writer has been unable to find representatives of this family in recent collections of free-living mites from Uganda, India, Singapore and Rennell Is.

DISCUSSION

The examination of the above mentioned species of the genera *Epicrius* and *Berlesiana* enables one to discuss in some detail the value of the morphological characters which have formed the bases of the various classifications of the *Epicriidae* put foward by previous workers. In several of these investigations, particularly those of Trägårdh, on the comparative morphology of the *Mesostigmata*, the classification has been built up on the evidence supplied by the critical examination of only one species, *Epicrius mollis* (Kr.). The following outline of the development of the classification of the family since its erection by Berlese (1885) will serve as the basis for discussion.

---

[1] Baker & Wharton (1952) state that " on Guam *Epicrius* sp. was found among the rhizomes of epiphitic ferns . . . " in which case this is the first record of the family outside the Palaearctic and Nearctic Regions.

Berlese (1885) considered the genus *Epicrius* and *Podocinium* Berl. to constitute a a subfamily (!) *Epicriidae* of the family *Gamasidae*. The characteristic features of this subfamily were the elongate first pair of ambulatory appendages and the ornamentation of the body of the mites. *Epicrius* and *Podocinium* were separated on the degree of development of the peritreme. Later (Berlese, 1892), *Epicrius* was placed with *Zercon* Koch and *Seiodes* Berl. in the *Zerconidae*, apparently on account of the position of the genital orifice in the male. This classification was retained by Berlese (1913) in his introduction to the " Acarotheca Italica," except that the *Zerconidae* was divided into the *Zerconini* and the *Epicriini*. Vitzthum (1929, 1931 and 1941) followed, in the main, Berlese's classification and at the same time emphasized the close relationship between the *Epicriidae* and the *Zerconidae*.

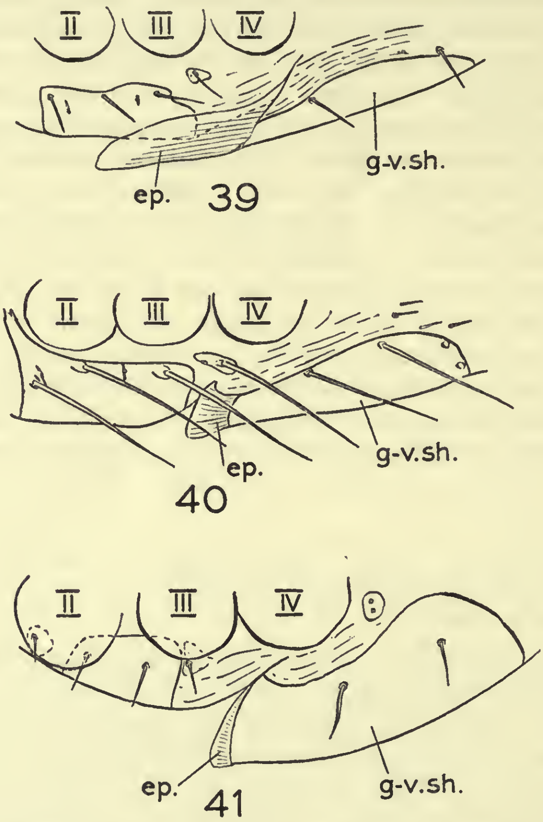
Trägårdh (1938), in the first of his important contributions to the classification of the *Mesostigmata*, separated the *Epicriidae* and the *Zerconidae*; placing the former in the SEJINA (= LIROASPINA) and the latter in the GAMASINA on differences in the structure of the genital and sternal regions in the females. The *Epicriidae* was regarded as a primitive group because of the absence of a distinct epigynal shield and the segmentation of the sternal region. The *Sejidae* (= *Liroaspidae*) and *Epicriidae* were separated as follows :

" A. Sternal shields III and IV fused, forming a narrow transverse shield, separated from the remaining sternal shield . . . . . Fam. *Sejidae*.
AA. All sternal shields fused . . . . Fam. *Epicriidae*."

In 1946 (1946*a*) the same general classification of the LIROASPINA was given except that the sternal region of the *Epicriidae* was now described as " sternal shields I free, shields II–IV fused." But after examining the structure of the genital region in the male, the *Epicriidae* was removed from the LIROASPINA to the EPICRIINA (Trägårdh, 1946*b*). At the same time the EPICRIINA was stated to resemble the ZERCONINA in this character. Therefore, the final result of Trägårdh's researches were to separate the *Epicriidae* and the *Zerconidae* into distinct cohorts, chiefly on the structure of the genital region in the females.

The writer disagreed with Trägårdh's interpretation of the structure of the genital region in the female of the *Epicriidae* and could find no evidence for his statement that an epigynal shield is not developed in this group (Evans, 1955). The genitiventral shield in both *Epicrius* and *Berlesiana* are basically the same as that in the *Laelaptoidea*. This is shown in Text-figs. 39–41, where a comparison is made between the genital region of two species of Laelaptoid mites and *E. mollis*. The writer therefore, suggested the inclusion of the *Epicriidae* and *Zerconidae* in the EPICRIINA, following Vitzthum (1941).

The second important morphological character used by Trägårdh in the classification of the LIROASPINA and EPICRIINA is the structure of the sternal shield in the females. It is on the basis of the degree of fragmentation of the sternal shield in the female that the *Epicriidae* was originally separated from the *Liroaspidae* and, later, the *Liroaspidae* from the *Epicrosejidae* (Trägårdh, 1952). This separation of the families appears to have been made after the examination of one species from each family. From the present revision of the *Epicriidae* it is quite obvious that the fragmentation of the sternal region in this group shows considerable variety and can no longer be used as a major character in the classification of the family. The following types of sternal " shields " were encountered in the females :



Text-figs. 39–41. Lateral view of the sterniti-geniti-ventral region of the females of two species of Laelaptoid mites (Figs. 39 and 40) and *Epicrius mollis* (Kr.), (Fig. 41). *ep.*, epigynal portion of the geniti-ventral shield ; *g-v-sh.*, geniti-ventral shield.

1. Sternal setae II free ; III and IV on a shield, (*E. minor*).
2. Sternal setae II and III on a shield ; IV free, (*E. mollis*, *B. denticulata*).
3. Sternal setae II, III and IV on a shield, (*E. canestrinii*, *E. menzeli*, *E. spinituberculatus*).
4. Sternal setae II, III and IV each on separate shield, (*B. cirrata*).

Jugularia are present in both sexes in all species.

The generic concept in the *Epicriidae* also has the structure of the sternal region in the females as its basis. In the recent classification given by Baker & Wharton (1952) the genera *Epicrius* and *Berlesiana* are placed in separate families ; the former in the *Epicriidae* and the latter in the *Liroaspidae*. In the present classification both genera have been included in the *Epicriidae* and the subgenera *Diepicrius* and *Epicriella* have been relegated to the synonymy.

SUMMARY

1. A revision is given of the family *Epicriidae* with a discussion on the classification of the EPICRIINA.

2. Two genera, *Epicrius* and *Berlesiana*, are considered valid. The former contains five valid species and three of uncertain status, and the latter two species.

3. Keys to species are given for the identification of both sexes of *Epicrius* and the females only of *Berlesiana*. *Epicrius* (*Diepicrius*) *parisiensis* Berl. is considered to be a synonym of *Epicrius canestrini* Haller.

4. The following two species are described as new : *Epicrius spinituberculatus* and *Berlesiana denticulata*.

ACKNOWLEDGMENTS

The writer is extremely grateful to Dr. Jos. Schweizer for the loan of material from his collection, to Dr. L. van der Hammen for specimens from the Oudemans Collection, to Dr. G. Lombardini for comparing specimens with those in the Berlese Collection, and especially to Dr. H. W. Parker for his criticisms of the manuscript.

The photographs are the work of Mr. M. G. Sawyers.

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EXPLANATION OF PLATES.

PLATE 1.

Ornamentation of the dorsal shield in *Epicrius mollis* (Kramer). × 1000.

PLATE 2.

Ornamentation of the dorsal shield in *Epicrius spinituberculatus* sp. n. × 800.

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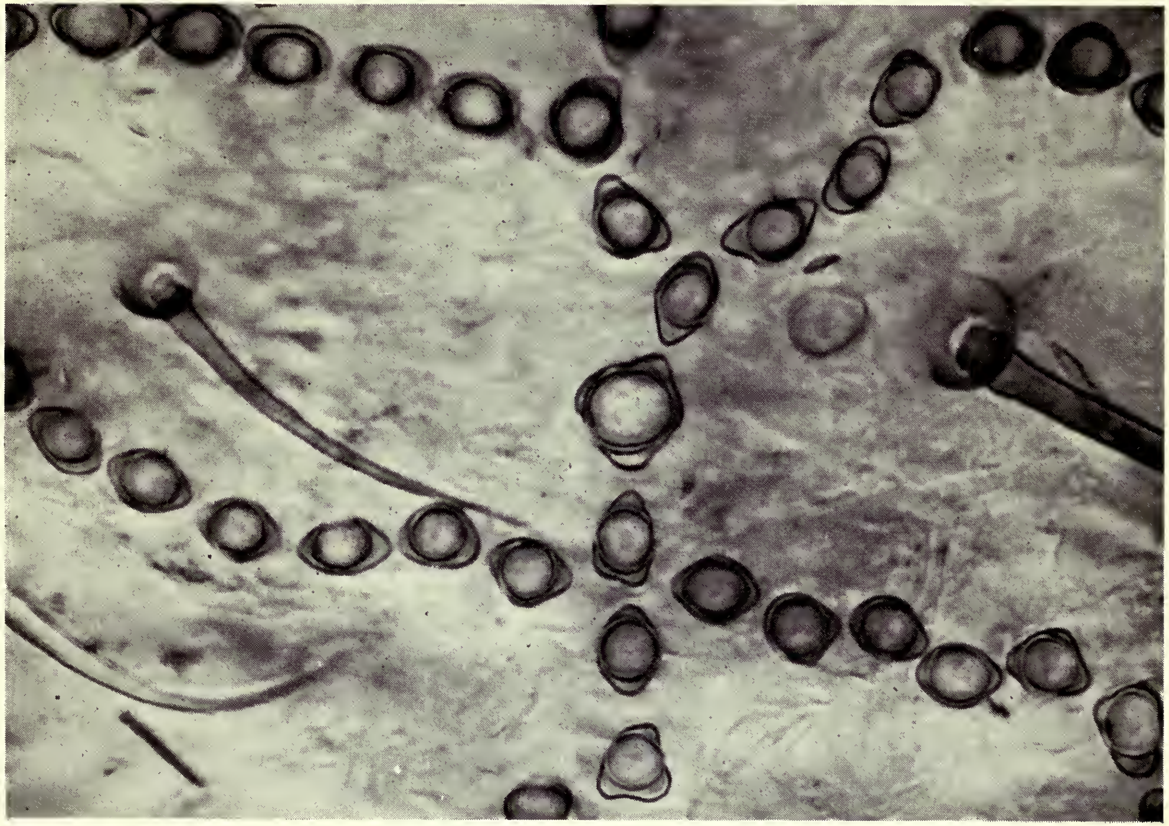
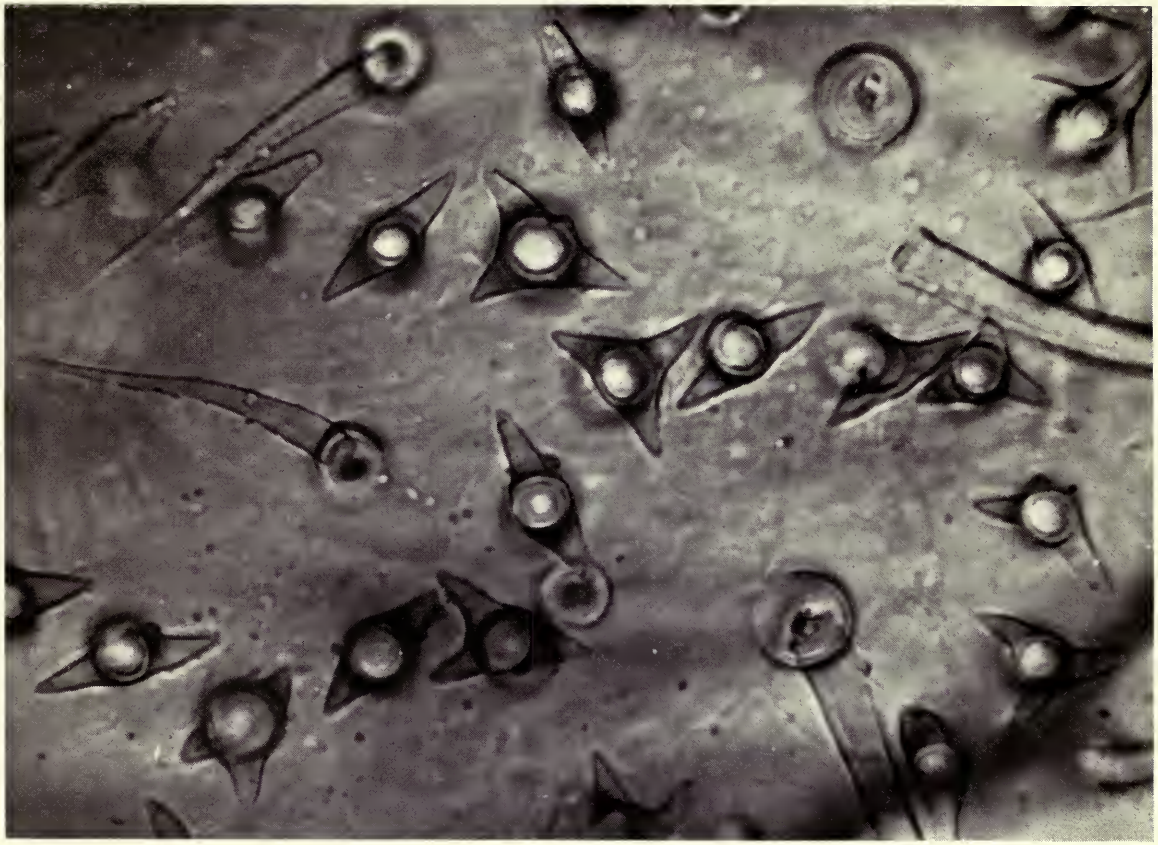
PLATE 1.



Epicrius mollis.



Epicrius spinituberculatus.

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THE MONK SEALS

(Genus *Monachus*)

JUDITH E. KING

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
ZOOLOGY Vol. 3 No. 5
LONDON: 1956

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(GENUS *MONACHUS*)

BY

JUDITH E. KING

Pp. 201–256 ; *Pls.* 3–8 ; 12 *Text-figures*

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THE MONK SEALS (Genus *Monachus*)

By JUDITH E. KING

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SYNOPSIS

An account is given of the history, distribution, features and habits of the three species of monk seal *Monachus monachus*, *M. tropicalis* and *M. schauinslandi*.

A list is given of the skulls, skeletons, skins and stuffed animals that have been examined.

The skull, dentition and skeleton are described and compared with those of other Phocidae. The members of the genus *Monachus* are shown to be much more nearly allied to the Southern than the Northern Phocids.

The relative growth rates of the various parts of the skull are given, and show that the facial region grows more quickly than the cranial region.

THE genus *Monachus*—the monk seals—consists of only three species. *M. monachus* (Hermann 1779) lives in the Mediterranean area, *M. tropicalis* (Gray 1850) in the West Indies, and *M. schauinslandi* Matschie 1905 in the Hawaiian Islands. They are interesting animals, but because of their widely scattered distribution, remoteness and scarcity, not a great deal is known about them. In this paper an attempt will be made to bring together as much information about the monk seals as it has been possible to find.

SYNONYMY

Genus ***MONACHUS*** Fleming, 1822

Monachus Fleming, 1822, *Philos. Zool.* **2** : 187 (footnote). *Phoca monachus* Hermann.
Pelagios F. Cuvier, 1824, *Mém. Mus. H.N. Paris*, **11** : 196. *Phoca monachus* Hermann.
Pelagius F. Cuvier, 1826, *Dict. Sci. Nat. Paris*, **39** : 550. For *Pelagios*.
Pelagus McMurtrie, 1834, Cuvier's *Animal Kingdom*, 71. For *Pelagios*.
Pelagias Gray, 1837, *Mag. Nat. Hist.*, N.S. **1** : 582. For *Pelagios*.
Pelagocyon Gloger, 1841, *Gemeinn. Naturgesch.* **1**, 34 : 163. *Phoca monachus* Hermann.
Rigoon Gistel, 1848, *Nat. Thier, für höhere Schulen. X.* New name for *Pelagios* F. Cuvier.
Heliophoca Gray, 1854, *Ann. Mag. Nat. Hist.* **13** : 201. *Heliophoca atlantica* Gray = *Phoca monachus* Hermann.

I. ***Monachus monachus*** (Hermann, 1779)

Phoca monachus Hermann, 1779, *Beschäf. Berlin Ges. Naturf. Freunde*, **4** : 501, pls. 12, 13.
Phoca albiventer Boddaert, 1785, *Elench. Anim.* **1** : 170.
Phoca bicolor Shaw, 1800, *General Zoology.* **1**, 2 : 254.
Phoca leucogaster Péron & Lesuer, 1816, *Voy. aux Terres Austr.* **2** : 47 (footnote).
Phoca hermanni Lesson, 1828, *Dict. Class. Hist. Nat.* **13** : 416.
Monachus mediterraneus Nilsson, 1838, *K. Svenska Vet. Ak. Handl.* **1837** : 238.
Phoca crinita Menis, 1848, *Il Mare Adriatico*, 153.
Heliophoca atlantica Gray, 1854, *Ann. Mag. Nat. Hist.* **13** : 202.

II. ***Monachus tropicalis*** (Gray, 1850)

Phoca tropicalis Gray, 1850, *Cat. Mamm. in colln. Brit. Mus.* part 2. Seals, 28.
—— *wilkianus* Gosse, 1851, *A Naturalist's Sojourn in Jamaica*, 308 (footnote).

III. ***Monachus schauinslandi*** Matschie, 1905

Monachus schauinslandi Matschie, 1905, *Sitzungs-Berichte der Gesellschaft Nat. Freunde*, Berlin, 258.

I. *Monachus monachus*

History

The monk seal appears to have been always well known to the inhabitants of the Mediterranean area. Clark (1952) notes that bones of this seal were found in upper palaeolithic levels at Grimaldi, and there is evidence that seal hunting was quite an important activity in classical Greece. The skins were collected partly for the superstitions surrounding them and partly for use as clothes by the poor fisher folk. Boots, tents and dresses made of skin were said to protect one from lightning ; a seal skin drawn round a field and then hung up by the door would save the field from hailstones, and the right flipper was supposed to be a cure for insomnia when put under the head at night. Greek writers such as Plutarch, Pliny, Homer and Aristotle knew and wrote of the seal. Aristotle must have examined one with care as he gives quite an accurate account in the *Historia Animalium*, but Keller (1887) says that on the whole the poets found the animal horrible and deformed, and objected to its oily smell. The presence of seals gave rise to many stories. The " half animal fisheaters " on the west coast of Africa were said to have made a pact with the seals not to interfere with each other's fishing, and in the *Odyssey* a woman who died on board ship was thrown overboard to serve as food for the seals and fishes. Because of their love of sun and sea the seals were put under the protection of Phoebus Apollo, the sun god, and Poseidon, the sea god. The seal was frequently shown alive in these times. Even then their docility and intelligence were noted, and Pliny tells how he saw some which answered by growls when their names were called. In earlier days there must have been more monk seals round the Greek coasts than there are now, as several towns have taken the name of the seal. Phocis is the name of an ancient Greek district that stretched past Mount Parnassus to the Gulf of Corinth, and there is at the present time Foca at the north end of the Izmir Gulf, Turkey, and Foča, an inland town in Yugoslavia. Keller (1887) notes that very ancient pre-Darian coins (*ca.* 500 B.C.) show a picture of a seal, and that coins from Rhodes show a seal's head. He also mentions that etymologically the Greek work for " phoca " means the swollen or plump animal, and must have been first applied, though not in a taxonomic sense, to the monk seal.

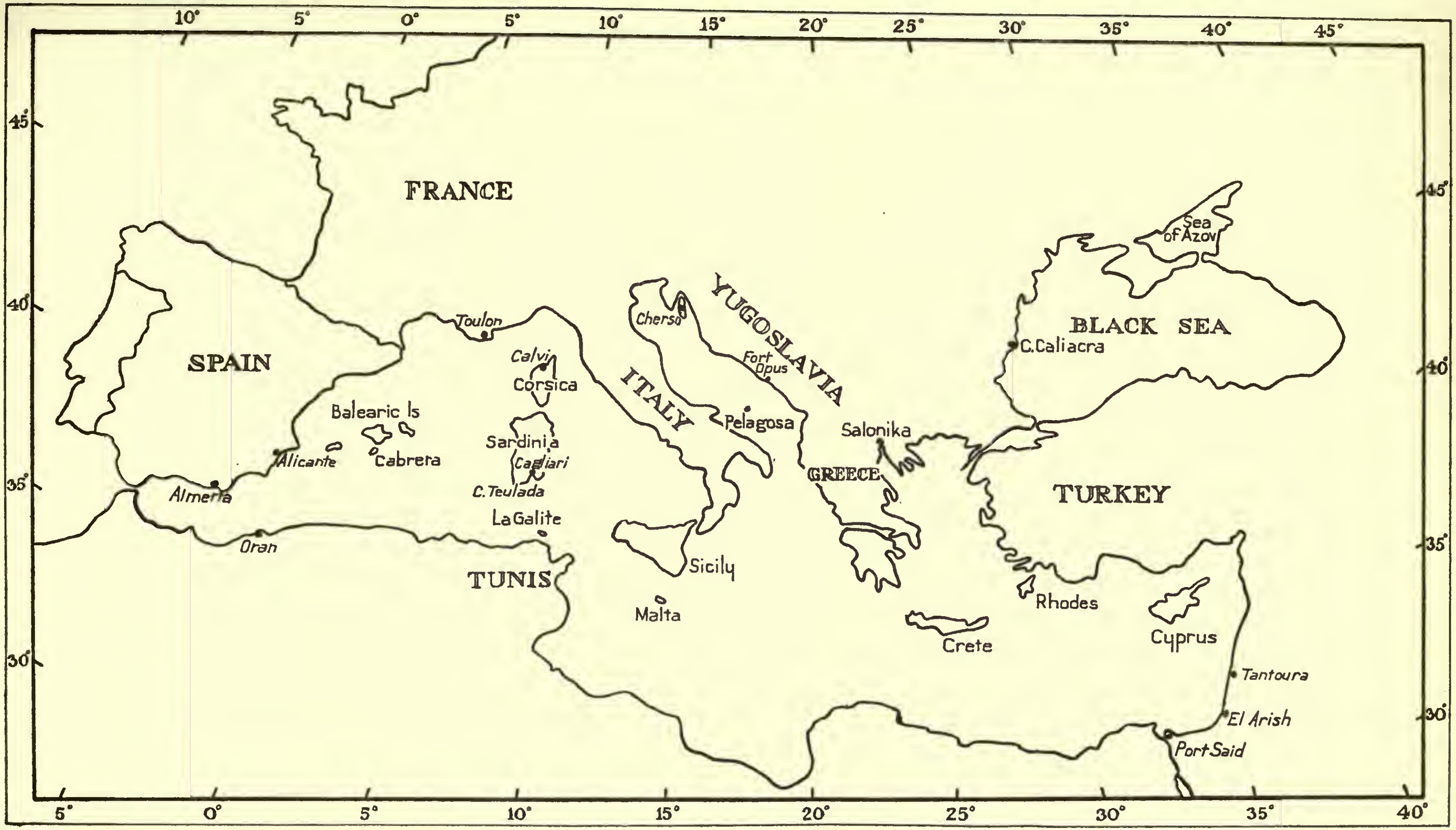
Some of the later history has been summarized by Monod (1932). An Italian map of the fourteenth century shows an island between Lanzarote and Fuerteventura in the Canary Islands called Ya de Uegi marini—the island of sea wolves—to-day called more simply Lobos Island ; and in 1341 Niccoloso di Recco included seals in an inventory of the Canary Islands. In the fifteenth century Portuguese explorers found numerous bands of monk seals and killed many for their skins, and in 1434 Alfonso Baldaya started the industrial exploitation of the seals in the bay Rio del Oro, north of Cap Blanc. A traveller named Zarco reached Madeira in 1418 and named a small cove Câmara de Lobos because of the seals he found there. Rondoletius published his *Aquatilium Historia* in 1554 and included a drawing and a short Latin description of " de Vitulo maris mediterranei ", but the first specific name was given by Hermann (1779) who described an animal from the Dalmatian coast and called it *Phoca monachus*. Buffon (1782) mentions that seals from the Adriatic were kept in captivity in France and Germany in 1760, and describes a female seal that was on exhibition in Nîmes in 1777. He also gives a detailed description of a male seal that was caught on 28th October, 1777, " off the island of Guarnero " in the Adriatic. He saw this seal in Paris in December, 1778, and from the similarity of his description of it and of its locality and habits it seems that it must have been the same animal described by Hermann—a fact which Cuvier noted as early as 1813. Hermann saw the seal in Strasbourg at the end of October and beginning of November, probably in 1778, and says that it was being taken on tour by a company of Venetians who were going to Paris to show it to the King. He mentions that the seal was said to have been captured in the autumn of 1777 in the Dalmatian Sea at Ossero. Ossero is on the island of Cherso in the Gulf of Quarnero, off the Dalmatian coast. Buffon notes that the seal died in August, 1779.

Since that time there have been many references, though mostly of the occurrence of single individuals. Cuvier (1813) describes a seal that was kept in captivity for two years in a very small bath, only a foot longer and two feet wider than the animal itself. In this remarkably small enclosure it spent 9–10 hours of each day in six inches of water that were drained off each night. The London Zoological Gardens has three times kept a monk seal for short periods. The first specimen, a young female, arrived in May, 1882, but died the same day ; the second was in 1894, when a young animal from Madeira lived there for three and a half months ; and the last was in 1910, when a second animal from Madeira lived for four months. In 1926 the American Museum of Natural History received skins and skeletons of three seals from the Desertas Islands ; these were believed to be the first Mediterranean seals in American museums. More recent references have again been concerned mainly with isolated occurrences, and there is at the time of writing a male monk seal from near Oran that has been in captivity for about two years in the Jardin des Plantes in Paris.

Distribution and abundance

The Mediterranean monk seal is known from the shores and islands of the Mediterranean and the western coast of North Africa (figs. 1 and 2). It has been recorded from : Gulf of Almeria, Spain ; Cabrera, Balearic Is. ; Toulon ; Corsica ; Cape Teulada and the Gulf of Cagliari in Sardinia ; the island of Pelagosa in the Adriatic ; the Gulf of Quarnero and Fort Opus in Yugoslavia along the Dalmatian coast ; the Gulf of Salonika in north Greece ; Cape Caliacra, and generally in the Black Sea and Bosphorus ; Tantoura ; El Arish ; Port Said ; the island of Galite off the Tunisian coast ; Oran ; Madeira and the Deserta Grande Islands ; the Canary Islands, and along the African coast, including Cap Barbas, Baie d'Etoile and Baie du Levrier, to Cap Blanc.

Budker (1945) says that the southern limit along the African coast is 20° 49′ N. (approximately the latitude of Cap Blanc), that its limit of distribution is influenced by the temperature of the sea and corresponds with the 20° C. winter isotherm. In the British Museum collections there is an Ascarid from a monk seal taken in Senegal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GREECE
Crete
BLACK SEA
C. Caliacra
Sea of Azov
TURKEY
Rhodes
Cyprus
Tantoura
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40°
35°
30°

FIG. 1.—Map of Mediterranean region to show distribution of *M. monachus*.

(approximate latitude 15° N.). It has been in the Museum since 1863, but there is no other information about the host.

Apart from the few references given by Monod (1932) for the fourteenth and fifteenth centuries there do not seem to be any other accounts of large scale commercial exploitation of the monk seal, although during a visit to Madeira in 1945, Cadogan (1945) heard that "in 1943–4 a consignment of some twenty-five seal pelts had been seized by the Customs Officials at Funchal, and it was not thought likely that any further attempt would be made to commercialize them for the present". Any commercial use of an animal necessarily implies its abundance in the area. Admiral W. H. Smyth, writing of the period 1810–1824 (in Flower, 1932) says that "between Alexandria and Benghazi . . . we found fish and seals in

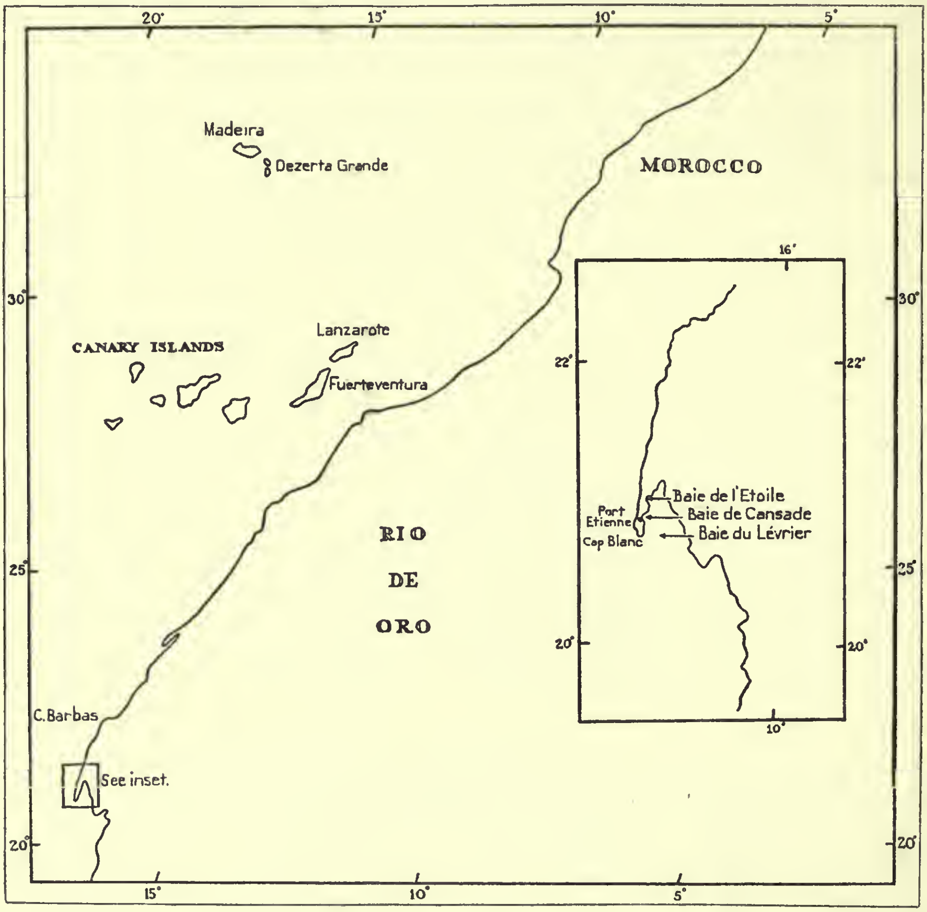
20°
15°
10°
5°
Madeira
Dezerta Grande
MOROCCO
30°
CANARY ISLANDS
Lanzarote
Fuerteventura
22°
16°
Baie de l'Etoile
Port Etienne
Baie de Cansade
Cap Blanc
Baie du Lévrier
RIO
DE
ORO
25°
20°
C. Barbas
See inset.
20°
15°
10°
5°
10°

FIG. 2.—Map of Mauritanean coast and Atlantic islands, and inset of Cap Blanc to show distribution of *M. monachus*.

abundance", but from then up to the present day there have been references only to single animals or small groups. Barceló (1875) said that seals were very common on the shores of the Balearic Islands at the time he wrote, but Cabrera writing in 1914 notes their disappearance from these parts. Aharoni (1930) notes that the seal is quite often offered for sale by fishermen from Askalon and Jaffa. Bertram (1943) says that a seal was seen off El Arish in about 1941, and according to Monod (1945), Agacino (1950) and Postel (1950) there must still be reasonably large colonies along the western coast of Africa down to Cap Blanc. Sixty seals were seen by Postel just north of Cap Blanc, and twenty-one by Agacino along the coast of Rio de Oro, and Cousteau and Dumas (1953) note the presence of a herd of about two hundred seals at Port Etienne. An adult female was surprised and killed in a cave in Corsica in 1947 (Troitzky, 1953), and Butler (in litt.) saw a seal in the Gulf of Salonika in 1950. There is still a small breeding colony in the more isolated regions of the Desertas Islands, although the fishermen there regard it as an enemy to their livelihood. A recent report in *The Times* (11th June, 1954) says that the monk seal still appears yearly on the Turkish coast. The main stronghold of the monk seal at present seems to be along the coast of Rio de Oro, and if not molested it is probable that its numbers will be maintained there.

Taxonomy

The first specific description of the monk seal is that given by Hermann in 1779. He named as *Phoca monachus* a male animal captured at Ossero, on the island of Cherso, off the Dalmatian coast in 1777, and seen by him in Strasbourg. He gives a very detailed description of the seal and its habits, and also a drawing of the whole animal with details of the head and flippers (Pl. 4, A). In 1782 Buffon, not knowing of Hermann's work, described the same seal which was, in 1778, on show in Paris. He gives a very good drawing of the animal (Pl. 4, B) but only refers to it as "Le phoque à ventre blanc". These two descriptions form the basis of practically all the succeeding names which have been applied to the monk seal.

Boddaert, in 1785, used Buffon's paper as the basis for his very brief Latin description of *Phoca albiventer*, a specific name which was in use for many years. In volume two of the third edition of Pennant's *Quadrupeds*, published in 1793, Pennant gives a description of the Pied Seal, mentioning Buffon, but adding "This I saw at Chester; it was taken near that city in May, 1766". It is difficult to know whether Pennant was applying Buffon's description to a seal actually taken near Chester, Cheshire, in which case it was very unlikely to have been a monk seal, or whether he was confusing the name with Cherso on the island of that name in the Adriatic. The drawing he gives is not very good, (Pl. 4, C) and shows an animal with a broad white ring round its neck and a white spot behind one flipper, the rest of the body being black. Pennant also describes the Mediterranean seal, quoting Hermann, but giving no picture. Shaw in 1800 uses Pennant's Pied Seal and Buffon's Phoque à ventre blanc for his *Phoca bicolor*, and used *Phoca monachus* for the Mediterranean seal. He uses the drawings previously given by Buffon and Pennant and labels both of them "Pied Seal var."

In a brief footnote, in which he quotes a passage from Buffon, Peron (1816) uses the name *Phoca leucogaster*, and in another equally brief footnote Fleming (1822) first suggests the use of the generic name *Monachus*, " Some seals, as *Ph. monachus*, are said to have four incisors in each jaw. Such will probably be constituted into a new genus, under the title *Monachus* ". In 1824 Cuvier suggested *Pelagios* as a new generic name for *Phoca monachus* Hermann, a name which has given rise to many variants ; Cuvier himself in 1826 called it *Pelagius*, McMurtrie (1834) used *Pelagus*, and Gray (1837) used *Pelagias*. Lesson in 1828 renamed Hermann's species *Phoca hermanni*, and Nilsson in 1838 called it *Monachus mediterraneus*. In 1841 Gloger called the monk seal of the Mediterranean *Pelagocyon monachus*, and in 1848 Menis used the name *Phoca crinita* for an animal presumably from the Adriatic (book not seen). Gistel, also in 1848, proposed the generic name *Rigoon* instead of *Pelagios* of Cuvier. Giebel (1848) linked the monk seals with the southern Phocids under the genus *Leptonyx* and the subgenus *Leptorhynchus*. This part of his classification is given here in full :

" *Leptonyx*
    a. Stenorhynchus
        1. L. serridens
        2. L. leopardinus
    b. Leptorhynchus
        3. L. weddellii
        4. L. rossii
        5. L. monachus."

The last synonym was given by Gray in 1854, when he named the new genus and species *Heliophoca atlantica* on the skin and skull of a young animal from Deserta Grande, Madeira. The skull and stuffed skin of this animal are now in the British Museum collections (Reg. No. 1853.10.6.4, 1063a.)

Description

Fully grown adults are about 8–9 ft. long. Gavard (1927) gives the length of a female which had produced a pup as 2·42 m. (7·9 ft.), but does not say whether this length included the hind flippers or not ; Troitzky (1953) gives the nose to tail length of an old female as 2·78 m. (9·1 ft.), and both Postel (1950) and Agacino (1950) note that the biggest animals that they saw were about 3 m. (9·8 ft.) long. Monod (1945) gives the length of a male animal as 2·9 m. (9·5 ft.). Of the two adult skins in the Museum collection the length of the male is 2·38 m. (7.8 ft.) and of the female 2·1 m. (6·9 ft.). These measurements are from nose to tip of tail, but should be regarded with caution as that of the male was taken from a rather crumpled dressed skin, and that of the female from an undressed but folded skin. The weight of the female seal measured by Gavard was 300 kilos (661 lb.), and that measured by Troitzky was 302 kilos (666 lb.) without the viscera.

There is a certain amount of variation in the colour of the adult seal. Gavard says that it is all black except for some patches, particularly a large one of a dirty white colour round the navel, and some little yellowish patches on top of the head. Agacino (1950) notes that the seal is spotted ventrally, but that there is some variation in colour and the old male may be a silvery colour all over. The light yellowish beige colour of the female described by Troitzky was also probably due to age. Cousteau and Dumas (1953) saw a large white bull in one of the caves on the islands of La Galite, but this may have been the silvery colour of old age. The monk seal now in the Jardin des Plantes in Paris is thought to be an adult animal and is chocolate brown dorsally shading to greyish fawn ventrally. It did not appear to have a white ventral patch but had several whitish scar marks along the back. An examination was made of the few skins of this species in the British Museum collections. The dressed skin of a fairly young male animal, length from nose to tip of tail 1·75 m. (5·74 ft.) (1894.7.27.3, 1063h), is dark blackish brown dorsally, with a slightly yellowish appearance due to the yellow tips of the dark brown hairs. This shades to light brownish yellow ventrally, but without a light ventral patch. The skin of an adult male (length 2·38 m., 1890.12.30.1) is generally dark blackish brown, slightly yellowish along the centre of the back and belly due to the yellow hair tips. In the centre of the belly, slightly nearer the fore flippers than the tail, is a roughly diamond-shaped patch of dirty yellow colour, about 73 cm. long and 58 cm. wide. The whole of the skin, particularly under the chin, the sides of the neck and the centre and hinder region of the back, is covered with irregularly placed streaks and spots of yellowish hair. These marks show on the under surface of the prepared skin and may possibly be due to scars. The skin of the adult female (length 2·1 m, 1894.7.27.2, 1063g) is more like the young animal than the adult male. It is dark blackish yellow dorsally, the hairs being dark brown with yellowish tips. This shades to light greyish yellow ventrally, and there is no light ventral patch. The back shows a few light scar-like streaks similar to those found on the male. These whitish streaks were also noticed on the seals examined by Hermann and Carruccio (1893); they are found on both sexes. The white ventral patch seems to be irregular in its occurrence.

The hairs of the adult are very short and bristly and lie close to the body. They are approximately half a centimetre long. The appearance of the young seal before it moults its natal coat is described from the youngest skin in the Museum collections (1892.11.7.1, 1063l). The length of the skin from nose to tip of tail is 1·4 m. (4.4 ft.). Dorsally it is a rich dark brown, shading at the level of the fore flippers to a lightish brown ventrally. On the belly, slightly nearer the fore flippers than the tail, is a roughly diamond-shaped patch of a dirty yellowish colour with a few very small light brown spots on it. The patch is approximately 34 cm. long and 28 cm. wide at its widest point. There is a small light brown area along the upper lip, and the whiskers are also light brown and oval in cross section. The texture of the hair of this young seal is quite different from that of the adult. It is soft and woolly, the hairs are 1–1½ cm. long and do not lie close to the body as they do in the adult.

The whiskers range in colour from light yellow to brown; they are smooth, not wavy as in *P. vitulina*, and oval in cross section. Nails are present on both fore and hind flippers. That on the first digit of the fore flipper is about 2·54 cm. (1 in.) long, and the others decrease slightly in size towards the fifth digit. The nails on the hind flippers are very small and inconspicuous. The tongue has a notch in its anterior end.

Lobstein (1817) described in some detail the anatomy of the viscera of a female seal that died in Strasbourg in 1815 after touring France and Germany for two years and Troitzky (1953) gives a brief description of the viscera of a full term foetus, but the most detailed recent investigation into the internal anatomy of *M. monachus* was done by Dieuzeide (1927) on a young male seal that was captured near Oran in December 1926, and which lived for a few months in the Experimental Station at Castiglione, Italy. A brief summary of the results, taken from Dieuzeide unless otherwise noted, is given here for completeness. The length of the male animal was 1·68 m. (5·5 ft.) from nose to tip of tail, and of Lobstein's female 2·13 m. (7·0 ft.). The oesophagus which lay mainly to the left of the trachea and large blood vessels was 60 cm. long and 4 cm. in diameter and was very dilatable. The oesophagus of the adult female (Lobstein) was 97 cm. long, the small intestine 14·5 m. and the large intestine 1·3 m. The whole alimentary canal was 17·5 m. (5·74 ft.)—eight times the length of the animal. There was no definite line of demarcation between the oesophagus and the stomach, which looked more like a dilatation of the oesophagus. The height of the stomach was about 25 cm., its width about 12 cm. and it led into the small intestine, which had a length of 12 m. and a diameter of 3–3½ cm. The caecum was a small pocket and the large intestine measured a metre in length by 4 cm. in diameter. The liver was large, measuring 40 × 40 cm. and consisted of six long pointed lobes. There was a large venous sinus (a dilatation of the inferior vena cava) and the round ligament (the remains of the umbilical vein) was well represented. The gall bladder was multilobulate and when full measured 13 × 13 mm. The left lung was the larger, weighing 950 gm., while the right weighed 850 gm. The kidneys were two oval masses, the right anterior to the left, with a combined weight of 1 kg. 140 gm. They were lobed and had an extensive vascular network. The left renal vein was large and of practically the same diameter as the vena cava. It was formed from the union of three large vessels and the superficial plexus of the kidney. On the right side the vena cava followed the inner border of the kidney and received vessels from it. The right kidney was supplied from the aorta by two renal arteries which arose a little anterior to the one going to the left kidney. The suprarenals were small and almond shaped, measuring 33 × 14 mm. The bladder was very thick (9 mm.) and measured 15 × 4 cm. The prostate was reduced and the testes were internal, measuring 4 × 1.5 cm. The penis was 8 cm. long and the baculum 7.8 cm. long. The heart was oval in shape, and Dieuzeide gives a detailed description of its anatomy.

Several species of parasites have been recorded from the stomach and intestine (Joyeux and Baer 1936, Baylis 1937, Markowski 1952). There are two Nematodes—*Contracaecum osculatum* (Rudolphi 1802) and *Porrocaecum decipiens* (Krabbe 1878), and four species of Cestode—*Diphyllobothrium coniceps* Linstow 1907, *D. elegans* (Krabbe 1865), *D. lanceolatum* (Krabbe 1865) and *D. hians* (Diesing 1850).

Remarkably little information is available about the breeding habits of this seal. Practically all that is known is in a recent paper by Troitzky (1953). In this she mentions that after a gestation period of eleven months the pups are born on land in September and October and are fed by the mother for six or seven weeks. The female has four teats on the posterior part of the abdomen and lies on her side when feeding the pup. At the end of this time the pup moults its woolly coat and enters the water for the first time. Troitzky says that the young seals stay with their mothers for three years, that they do not begin to breed until they are four years old, and that mating of the adult animals takes place about seven or eight weeks after the birth of the pup. The sum of eleven months' gestation plus seven or eight weeks before mating makes a total breeding cycle of thirteen months, and although it is usual in most Phocids for the female to bear a pup at the same time every year, Troitzky says that this seal only has a pup every alternate year.

Apart from Troitzky's paper, most of the information about breeding times has to be inferred from records of still born pups, foetuses and young animals. Dathe (1934) records that a young female seal was caught on 19th September, 1933, on the Dalmatian coast. The umbilicus was not yet healed and the animal was thought to be only a few days old. Its length was approximately 90 cm. and it weighed 26 kilos. This little animal was kept in captivity and was going to be taken to Frankfurt Zoological Gardens. It was fed by bottle six or seven times a day on a mixture of half gruel and half milk with a little cod liver oil and freshly rubbed fish paste. On 26th September it was taken to Split, preparatory to moving to Frankfurt, but the journey re-opened a wound on its stomach, caused probably by a fish hook, and on 29th September it died, its length then being 1.20 m.

Carruccio (1893) notes that a foetus 50 cm. long was taken from a pregnant female on 21st May, 1891, and Gavard (1927) mentions a captive female that produced a still-born pup on 14th April, 1926. This pup weighed 2.25 kilos and measured 62 cm. Both these foetuses are of such a size that they would have been full term and born about September, and it is strange that Postel (1950) should say that the pups are born in the spring. Agacino (1950), who went to Las Cuevecillas, Rio do Oro on 26th December, 1945, says that at that time the smallest seals were 1.5 m. long, and that a mother was seen to be feeding her pup. This must have been a pup born very late in the season, probably about the middle of November.

The voice is said to be a sharp strong cry from the bottom of the throat (Cuvier, 1813), while Agacino (1950) says that when they are annoyed they make a noise like a wounded dog. Hermann said that the one he observed had a voice like that of a hoarse dog and that sometimes it would howl. This seal could not tolerate dogs, and would try to drive them away by clapping its teeth. The seals kept in captivity have all been noticeably intelligent and docile animals. They have become attached to their keeper and would recognize him, follow him about, and even obey his orders to a certain extent.

The feeding habits, as observed in captivity, are very interesting. The animal described by Hermann ate about 14 pounds of fish daily and in order to stress the expense of keeping it, inquisitive spectators were told that it ate only the best fish, such as eels and trout. It did occasionally receive eels and carp, if paid for by the spectators, but usually it had whiting. It took the fish either out of the keeper's hands or caught them in its tank, but preferred to eat them in water. It seized the fish by the head, squeezed and shook them a few times and then swallowed them whole. Often intestines of the fish were found in the water, and although the keeper thought this was done deliberately, Hermann suggested that the insides of the fish came out accidentally when it was squeezed. Buffon saw the same animal while in Paris and said that there it was fed mainly on carp and eels, preferring the latter. The fish were sprinked with salt, the eels eaten whole, but the carp were crushed with the teeth, let fall and then the belly of the fish ripped open and the entrails removed. The fish was then seized by the head and swallowed. Cuvier also notes that the entrails were removed and the fish swallowed head first. The seal at present in Paris was also seen to swallow its fish head first, and this has also been observed in *Halichoerus grypus* and *Phoca vitulina*. Indeed it seems possible that this method might be the normal one for Pinnipeds generally, as it would avoid any injury to the seal by the backwardly projecting fins, scales and spines of the fish. Two female seals described by Gavard (1927) also disembowelled their fish unless they were very small, and also were unable to pick the fish off the ground, and could eat them only in water. They ate sardines, bonito and octopus—about 12 kg. a day. Boettger (1951) notes that native fishermen along the African coast say that the seals eat fish and lobsters (*Palinurus*), and remains of fish of the genera *Dentex* and *Labrax* have been found in the stomach of a seal captured off Sardinia (Carruccio 1893). A monk seal in the Gulf of Salonika was seen to be playing with a large fish, tossing it into the air and catching it again (Butler in litt.)

Troitzky (1953) describes an adult female seal that was killed in a cave on Corsica in September, 1947. It was found to be pregnant and a full-term foetus was removed, but could not be revived. The pup, a female, was 120 cm. long and weighed 17 kilos. It was dark, greyish black colour, with a white ventral patch. Troitzky notes that the pup in its colouring did not differ from descriptions of what she regarded as "typical" *M. monachus*, but says that the mother was not so. She observes that in its dentition, its great size, and the time of breeding the adult resembles *M. monachus*, but the shape of its head with a long snout, the light colour, the absence of the white ventral patch, and the second digit of the fore flipper longer than the first are characters not associated with that species. After reviewing other members of the Phocidae she comes to the conclusion that these characters are more like those of Arctic Phocids, and says that the most logical conclusion is that this female is a hybrid, the result of a cross between a monk seal and, probably, *Phoca groenlandica*, and that it is interesting that such a hybrid should have been able to produce a pup.

It is considered extremely unlikely that such a cross could have taken place. *Phoca groenlandica* and other members of the Arctic Phocidae have not been recorded from the Mediterranean in Recent times, and indeed, they seldom occur south of Arctic latitudes. From the description of the teeth—worn, broken and diseased—it is assumed that the animal was old, and the light colouring was probably also due to age. The white ventral patch is not of universal occurrence amongst the monk seals. It is not possible to comment on the other two characters, from lack of exact information, but from the photograph of the adult seal, as far as it is possible to see the shape of the fore flipper does not appear to be unusual and the drawings and photograph of the skull do not appear to differ in any way from undoubted skulls of *M. monachus* in the Museum collection.

II. *Monachus tropicalis*

History

The first reference to the monk seal of the West Indies is that given in the account of the second voyage of Columbus. At the end of August, 1494, the ship anchored by the rocky island of Alta Vela, south of Haiti (= Hispaniola), and the men that went ashore killed eight " sea wolves " that lay sleeping on the sand (Kerr, 1824). The next record chronologically, and the first for Florida, is that of Herrera who, while describing Ponce de Leon's discovery of the Dry Tortugas Islands (lat. 24° 10′ N. long. 83° 55′ W.) on 21st June, 1513, said that a foraging shore party took fourteen seals (Moore 1953). Du Tertre (1667) was told by Brother Charles Poncet, who had been to Guadeloupe, that he had seen at least twenty asleep under the trees near the shore, and many of them were killed. Dampier (1705) noted that there were seals on the Alacrane Islands in 1675, Sloane (1707) saw them on the Bahama Islands in 1687, and Olafsen (1774) makes a reference to the seal of the Antilles. Hill (1843) gives a description of a young seal from Pedro Kays, and Gosse (1851) published an account of a voyage in 1846 by Mr. George Wilkie to Pedro Kays, where he saw several seals and killed a few. It was on this voyage that the type skin of *Phoca tropicalis* was obtained. In 1883 the U.S. National Museum received a mounted skull and skin from a female seal captured off Cuba earlier in the same year and presented by Prof. Felipé Poey (True and Lucas, 1885). In 1886 H. L. Ward and Prof. F. Ferrari Perez of the Mexican Geographical and Exploring Survey set out from Campeche to the Triangles to search for *Monachus*. (Ward, 1887b). Although they were only on the islands from 1st to 4th December, forty two specimens were taken away and shared between the two members of the expedition. Of the specimens retained by H. L. Ward a complete articulated specimen (1887.8.5.1), and a skin and skull (1889.11.5.1) are now in the British Museum (Natural History), and an articulated specimen (899c) is in the Cambridge Zoological Museum. These last two specimens were purchased from Ward by F. D. Godman of Cambridge. A recently born pup was taken back to Campeche, but it lived there only a week. A female seal was captured at the Triangles in 1897 and lived for nearly 5½ years in New York Aquarium, where it died in 1903. (Anon 1903). E. W. Nelson and E. A. Goldman, during their biological investigations of Mexico from 1892 to 1906 (Goldman, 1951), spent the period 18th to 23rd June, 1900, on the Triangles. Their main object there was to obtain specimens of seals, but apart from remarking that " in quest of these animals we were very successful ", no mention is made of their abundance, or how many were killed. The New York Aquarium received four more seals—an adult male and three yearlings—in June, 1909 (Townsend 1909). These were obtained from a dealer in Yucatan who presumably got them from from the Triangles or the Alacrane Islands. Several seals were seen on the Tortugas Islands during the period 1903–8 and two were kept in a moat for some time, where they became fairly tame (Moore, 1953). Six seals were captured by a fishing vessel in 1915 and taken to Pensacola, where they were kept in captivity for some time and then turned loose, when bathers in the area objected to their presence (Allen 1942). Townsend (1923) notes that a seal was killed near Key West, Florida in March, 1922. Gunter (1947) gives sight records of seals along the Texas coast in 1926 and 1932, and Lewis (1948) says that a young seal was killed at South West Kay in the Pedro Group in 1939. A. C. Wheeler (in litt.) saw two seals on the beach of Drunken Man's Cay, about two miles south of Kingston, Jamaica in November, 1949.

Distribution and abundance

The West Indian monk seal was at one time abundant in the Gulf of Mexico and off the islands in the Caribbean Sea (Fig. 3.). The presence of numerous Seal Cays and Islands and Lobos Cays show how widely the seal was distributed in the area.

1. Seal Cay, south of Long Island, Bahamas. lat. 22° 38′ N., long. 75° 54′ W.
2. Seal Cay, south of Caicos Bank, Bahamas lat. 21° 10′ N, long. 71° 47′ W.
3. Seal Island, north of Anguilla, Leeward Is, W. Indies lat. 18° 24′ N., long. 63° 20′ W.
4. Cay Lobos, north of Cuba, lat. 22° 25′ N., long. 77° 36′ W.

and Allen (1887*a*) gives the following :

5. Seal Keys—on the coast of Honduras in about lat. 16° N., a few miles north-east of the Mosquito Coast.
6. Seal Key—about 200 miles further south along the same coast in about lat. 12° 40′ N.

It has been recorded from the Bahama Islands ; Key West, Florida ; Galveston Bay and Brazos, Texas ; the Triangle Islands to the west of Yucatan, lat. 20° 55′ N. long. 92° 12′ W. : the Alacrane reef to the north of Yucatan, lat. 22° 32′ N., long. 89° 45′ W. ; the shores of Cuba and Jamaica ; the Pedro Kays to the south of Jamaica, lat. 17° N., long. 77° 30′ W. ; Alta Vela, a rocky island south of Haiti ; and Guadeloupe.

That the seal has formerly been abundant is evident from some of the earlier accounts. Dampier (1705) said of his visit to the Alacranes in 1675 : " Here are many seals . . . the Spaniards do often come hither to make Oyl of their Fat ; upon which account it has been visited by English-men from Jamaica, particularly by Capt. Long : who having the Command of a small Bark, came hither purposely to make Seal-Oyl." Sloane (1707) gives the following account of the seals of the Bahamas, " The Bahama Islands are fill'd with Seals, sometimes Fishers will catch one hundred in a night. They try or melt them, and bring off their Oil for Lamps to these Islands." In 1856 a Mr. Alexander was on the Triangles and saw only two

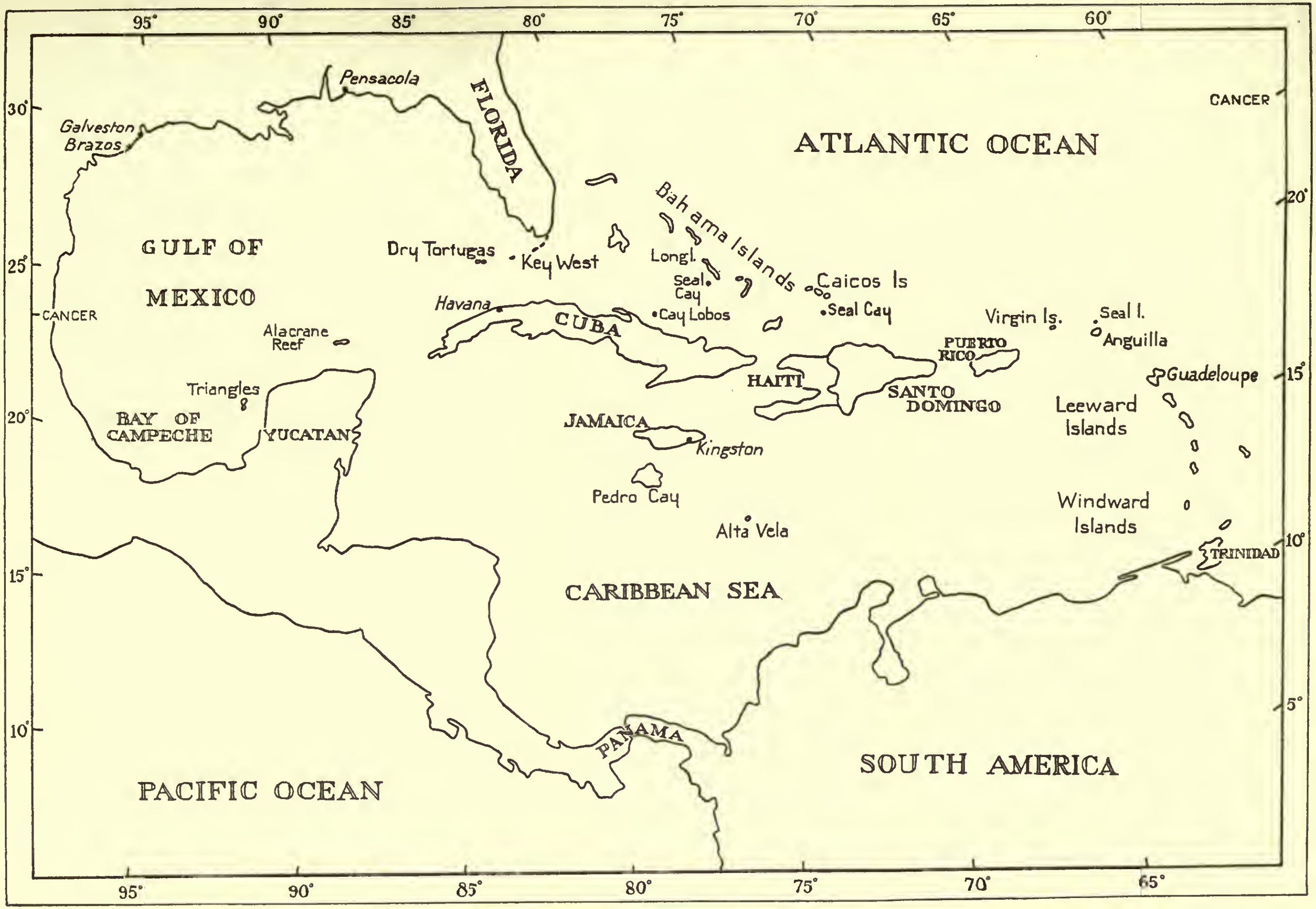
95°
90°
85°
80°
75°
70°
65°
60°
30°
25°
20°
15°
10°
5°
CANCER
CANCER
ATLANTIC OCEAN
Pensacola
FLORIDA
Galveston
Brazos
GULF OF
MEXICO
Dry Tortugas
Key West
Bahama Islands
Long I.
Seal Cay
Cay Lobos
Caicos Is
Seal Cay
Havana
CUBA
Alacrane Reef
Triangles
BAY OF CAMPECHE
YUCATAN
HAITI
SANTO DOMINGO
PUERTO RICO
Virgin Is.
Seal I.
Anguilla
Guadeloupe
Leeward Islands
Windward Islands
TRINIDAD
JAMAICA
Kingston
Pedro Cay
Alta Vela
CARIBBEAN SEA
PANAMA
SOUTH AMERICA
PACIFIC OCEAN

FIG. 3.—Map of Caribbean region to show distribution of *M. tropicalis*.

living seals, but remains of skeletons and hides indicated a once flourishing business; and although H. L. Ward does not say exactly how many he saw in 1886, there must have been quite a large colony as he killed over forty animals (Ward, 1887*b*). Allen (1887*a*) suggested that at the time of his writing seals were still present on the islets of Salt Key Bank, north of Cuba, the isles off Yucatan, and probably the isles between. In 1897 at the time of the capture of the seal for New York Aquarium about thirty were observed on the Triangles (Anon 1903), but as late as January, 1911, according to Lewis (1948) about two hundred seals were killed in this locality and at the time his paper was published he thought that there were perhaps still a few left there and on the South West Kay in the Pedro Group. In view of the fact that seals have been seen as recently as 1949 near Jamaica, and that Moore (1953) quotes a " well informed and responsible friend " who knows of the whereabouts of seals somewhere within their former range, it seems likely that a remnant of this species is still living.

Taxonomy

During Mr. George Wilkie's visit to the Pedro Kays in 1846 (Gosse, 1851) he obtained the skin of a monk seal which he gave to Gosse. Gosse sent this skin, which had no bones with it, to the British Museum where J. E. Gray published a description of it under the name *Phoca tropicalis* Gray, 1850. This skin has been stuffed and is in the Museum collection (Reg. No. 1847.2.2.2). Gosse (1851) republished the description of the seal given by Hill (1843), and in a footnote on p. 308 suggested the specific epithet " *wilkianus* ", but he gave no generic name, and moreover, was already antedated by Gray. In 1866 in the *Catalogue of the Seals and Whales in the British Museum* Gray repeated the descriptive paragraph he gave in 1850, but used the name *Monachus tropicalis*.

Description

The nose to tail length of an adult male animal is between 7 and 8 ft., females being in general slightly smaller. Townsend (1906) gives the length of an old female with very worn teeth as 9 ft., but he was probably measuring to the tips of the hind flippers. The nose to tail lengths of both the skeleton in the British Museum, (probably a female) and that in Cambridge, (sex unknown) are both about 7 ft. 3 in. The nose to tail length of a dressed skin of an adult male (1889.11.5.1, 1064b) is 7 ft. 5 in., and Ward (1887*b*) gives nose to tail lengths of two pregnant females as 7 ft. 1 in. and 6 ft. 6 in. A female measuring 6 ft. 11 in. to the tip of the hind flippers and which had been in New York Aquarium for 5½ years weighed 360 pounds at death. This seal died from fatty degeneration of the heart, liver and kidneys, so presumably a healthy animal of this size would weigh less.

Ward (1887*b*) gives the following description of the colour of the adult seal: " Adults are grayish brown or grisled on the back, a result of the Vandyke-brown hairs being tipped with light horn-color, the lower surface ochreous yellow to yellowish white. Females seem to have much less of the yellow or white on the ventral surface. From the black pelage of the extremely young to that of the adult there is an intermediate stage of yellowish gray on the dorsal surface, shading to almost a perfect ochre on the ventral portions." This is the most reliable account of the colour, and corresponds well with that of the stuffed specimen in the Museum, which is the type of *Phoca tropicalis* Gray. This animal is dark brown, and slightly lighter on the sides and belly. The hairs of the back are dark brown with a lighter tip, while those of the sides and belly have a more yellow tip. The hairs lie close to the body and are extremely short, the longest—those on the sides—being about 1 cm. long. A dressed skin of an adult male from the Triangles in the Museum collection (1889.11.5.1, 1064b) is dark blackish brown all over, with a slight yellowish tinge due to the yellow tips of the hairs. New born pups are black in colour and the hair is long, soft and woolly.

The whiskers are yellowish horn colour, some being slightly darker at their bases. Those of the Museum specimens are oval in cross section. Nails of appreciable size are present only on the fore flippers. That on the first digit is about an inch long, those on the remaining four digits decreasing gradually in size. The nails of the hind flipper are very small.

The description of the eye is given by Ward (1887*b*): " The pupil is medium sized, round, and well defined, the iris is light reddish brown in color, and with but little of the sclerotic coat showing. Over the cornea there appears a deadening film . . .", which he attributes to the strong reflection of the tropical sun from the coral sands.

Young animals are born about the beginning of December. Ward (1887*b*) was on the Triangles from 1st to 4th December and killed five females with full-term foetuses, and noticed another female with a new-born pup. The female has four teats. One of the foetuses measured 85 cm. from nose to tip of tail, was covered in black woolly hair and had black whiskers. Measurements of the skull and skeleton of this pup as well as those of adult animals collected by Ward are given by Allen (1887*a*).

Ward examined the stomach contents of several animals, but found only fluids and large numbers of intestinal parasites several inches in length. Gosse (1851) recorded the opinion of the " more experienced fishermen ", who said that the seals fed " as generally on molluscous animals as on fish ", but there is no proof of this. The animal noted by Hill (1843) lived for four months in captivity, without eating, and when it died " the fat was four inches thick and yielded four gallons of oil ". The skull of this animal, which was then, as Hill (1846) says " an undescribed Seal ", was exhibited at a meeting of the Zoological Society of London in September, 1846. Unfortunately it has not been possible to trace this skull, which was probably the first specimen of the West Indian monk seal to reach this country, arriving here shortly before the skin sent by Gosse which became the type.

The West Indian monk seal appears to be a fairly noisy animal. Hill (1843) said that his young animal " grunted, barked, growled and snarled like a dog ", and Ward (1887*b*) said that the voice of the young was " a long drawn out guttural ' ah ' with a series of vocal hitches during its enunciation ". Townsend (1909) also noted that it was noisy, and the young often roared harshly.

On land at least the seal seems to be rather lethargic. Ward (1887*b*) notes that unless the seals were approached closer than three or four feet they showed no interest or alarm. Closer than that they would rouse themselves, bark, and move off a little. When Ward and his party attacked a group of seals they got more excited and would make savage rushes, and would then fall back on their dead fellows and bite and shake them. Nevertheless, as Ward notes " the whole aspect of the animals was one of indecision . . . they only roused themselves to action on being individually attacked ". This behaviour is not peculiar to the monk seal, but seems to be common to all seals. Ward also notes the peculiar circumstance that several of the animals he collected had a growth of minute algae upon their backs and flippers, especially the hinder ones, so that they appeared quite green.

Although Ward says they are neither curious nor playful, Hill (1843) notes that the young specimen he kept in captivity was lively, and those kept in New York Aquarium were certainly playful. The two which were received in 1897 had the habit of filling their cheeks with water and squirting it at visitors, while the seal which arrived in 1909 amused itself by tossing flipperfuls of water into the faces of visitors.

III. *Monachus schauinslandi*

History

The Hawaiian or Sandwich Islands are a chain of small islands near the centre of the North Pacific Ocean between 18° 55′ and 28° 25′ N., and 154° 48′ and 178° 25′ W. (Text-fig. 4) ; Honolulu on the island of Oahu being 2,100 miles S.W. from San Francisco and 3,445 miles S.E. from Yokohama. The chain stretches 1,578 miles from E.S.E. to W.N.W. All the islands are uninhabited, except Midway which is a transpacific cable station and sea plane base administered by the U.S. Navy, and Niihau, Kauai, Oahu, Molokai, Maui and Hawaii. The entire chain forms the Hawaiian Islands Bird Reservation.

Perhaps owing to the remoteness of the islands on which they live, there are very few references to the Laysan monk seal. In the early part of the nineteenth century seals must have been numerous as Bryan (1915) records that in 1824 the brig " Ainoa " set out from Hawaii on a sealing voyage in that area, and in 1859 the " Gambia " returned to Honolulu with 1,500 seal skins and 240 barrels of seal oil, some of which was probably from Midway Id., which was discovered on this trip. In 1893 a Mr. J. J. Williams visited Laysan and heard of an earlier expedition that had killed sixty or seventy seals on the island (Atkinson and Bryan, 1913). In 1905 Matschie published a description of a seal skull brought back from Laysan by Dr. H. Schauinsland, and named it after him. The U.S. revenue cutter " Thetis " returned in 1912 after a cruise to Midway and Laysan and brought back a seal skin which was presented to the Bishop Museum in Honolulu (Bryan, 1915) and parts of three others which are in The U.S. National Museum. Thirty five seals were seen on Pearl and Hermes Reef in 1913 (Atkinson and Bryan 1913), and Dr. Wetmore, who visited the area with the U.S.S. "Tanager" Expedition in 1923 saw a number of seals and collected ten for the U.S. National Museum (Bailey, 1952). In 1940 about

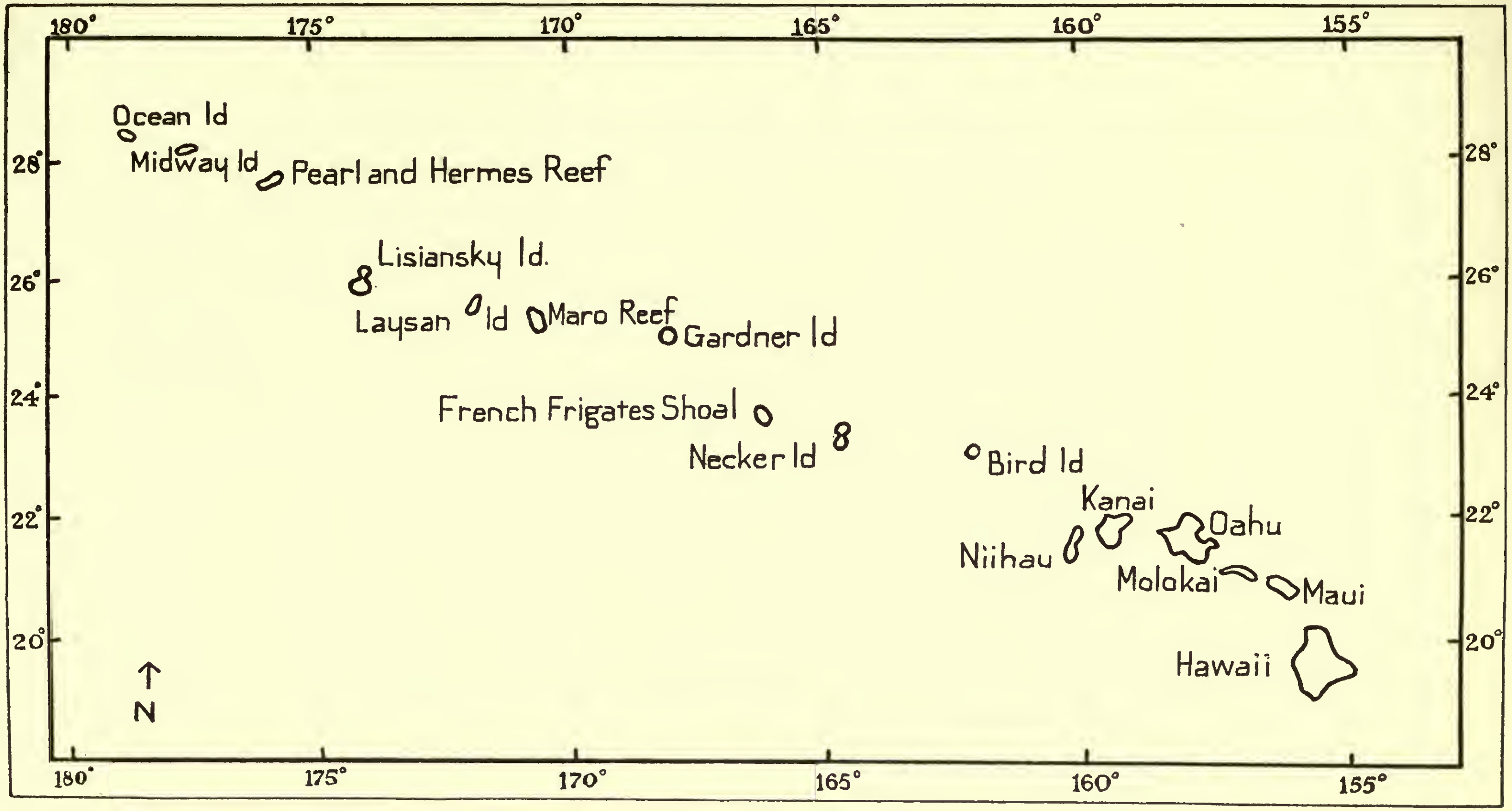
180°
175°
170°
165°
160°
155°
28°
26°
24°
22°
20°
Ocean Id
Midway Id
Pearl and Hermes Reef
Lisiansky Id.
Laysan Id
Maro Reef
Gardner Id
French Frigates Shoal
Necker Id
Bird Id
Kanai
Niihau
Oahu
Molokai
Maui
Hawaii
N

FIG. 4.—Map of the Hawaiian or Sandwich Islands to show distribution of *M. schauinslandi*.

half a dozen were seen round Midway (Blackman, 1941) and records of visits to the islands in 1949 and 1951 show that quite large numbers were seen resting on the beaches. The first, and it is believed, the only seal of this species to be kept in captivity outside the Hawaiian Islands was a young animal which was presented to San Diego Zoo by the Honolulu Zoo in 1951 (Anon, 1951). It was captured on French Frigates Shoal but only lived about three months in captivity.

Distribution and abundance

The Laysan seal has been recorded from the following of the Hawaiian islands: Ocean Island, Midway Island, Pearl and Hermes Reef, Lisiansky Island, Laysan Island, French Frigates Shoal, and a stray animal has been recorded from the coast of Hawaii, although they do not generally appear to go so far eastwards.

In 1824, 1859 and 1893 the seals were obviously very numerous, although in Schauinsland's own account of his visit to Laysan (Schauinsland, 1899) he only mentions that "seals come singly, indeed very seldom by the island". In 1912, Elschner (1915) who was also on the "Thetis" during its trip, noted that there were many seals on French Frigates Shoal and Pearl and Hermes Reef. Also on the latter island thirty five seals were seen in 1913 (Atkinson and Bryan, 1913). The U.S.S. "Tanager" Expedition sailed from Honolulu in April, 1923, for a visit to the Hawaiian Islands. The *Bulletin of the Bishop Museum* in Honolulu (Bull. 10, 1924) only mentions that several seals were seen on Lisiansky on this voyage, and that two skins and skulls were collected; Allen (1942) however, notes that Dr. A. Wetmore while on this expedition saw colonies of seals on Pearl and Hermes Reef and on Ocean Island, and estimated the total population to be about four hundred, and Bailey (1952) notes that he brought back ten specimens for The U.S. National Museum. Sixty eight seals were seen on Pearl and Hermes Reef in 1930, and five on Laysan in 1936 (Bailey, 1952), and Blackman (1941) who stayed for six months on Midway in 1939–40 saw about six seals. More recent visits to the islands (Bailey, 1952) show that the animals are still fairly numerous there. About thirty were seen on Laysan and over a hundred on Midway. A count of seals made in 1951 showed a total of 407 on the beaches, the largest populations being on Laysan (119) and Pearl and Hermes Reef (180). The others were seen on French Frigates Shoal, Maro Reef, Lisiansky and Midway. It was suggested that the large numbers on the beaches could perhaps be accounted for by the presence of tiger sharks in the water.

The monk seals are distinctive in being the only truly warm water form of Phocid, with the exception of the northern elephant seal (*Mirounga angustirostris*). So far as the distribution of the three species is concerned it is not difficult to accept the occupation of the West Indian islands from a source in the Mediterranean and along the Mauritanian coast, as the Canary Current passing down the latter coast would bear the emigrants to the eastern limit of the North Equatorial Current sweeping due west to the Caribbean Sea. The extension of the range of the genus to Hawaii and across the Isthmus of Panama is feasible when it is accepted that Phocids are capable of considerable overland journeys. For example Hayes (1928, p. 106) records that Captain Scott, when in the Antarctic, found seal carcases as far as fifty miles inland

and 5,000 ft. above the sea. The Isthmus of Panama at its narrowest is much less than fifty miles, and its lowest height above sea level less than 200 ft. If rivers were exploited by the seals the distances travelled overland might have been still further diminished. The North Equatorial Current in the Pacific could well have borne the animals to the islands they now occupy. Allen (1942) suggests that the colonization of the Pacific by the monk seal was from the West Indian stock in Tertiary time, when there was a waterway connecting the Atlantic and Pacific.

Description

Of the few records available only those of Matschie and Bailey (1952) give any information about the external features and Bailey includes some excellent photographs. A male, probably not full grown, collected by the " Thetis " measured 5·7 ft. from tip of nose to tip of tail, and a female 7·5 ft. Matschie gives the following description : " A scalp which I have for examination has very short, thick, bristly hair, loam coloured, with a silky shine. The lips are yellow-gray, and it is somewhat brownish on the front side of the neck. Most of the whiskers are light horn coloured, a few dark brown, and all with very thin points. The sides of the body of the stuffed animal in Bremen Museum are lighter than the back, the breast and stomach are whitish." Bailey notes that the underparts are light straw yellow and the back is dark slate grey.

While on the " Tanager " Expedition Dr. Wetmore examined the stomachs of seals for parasites. All the seals had abundant nematodes in the stomach and Chapin (1925) has described these as a new species *Contracaecum turgidum*. Cestodes, *Diphyllobothrium hians*, were also found.

The birth of the young seals evidently takes in January. The " Thetis " saw pups at this time in 1912, and one was born during the visit of Governor Frear to Pearl and Hermes Reef in January, 1913 (Atkinson and Bryan, 1913). The young male seal that lived in San Diego Zoo for a short time (Anon, 1951) was received in May and died probably at the beginning of September. It was therefore about eight months old at the time of its death. It is described as a nursing pup of approximately three feet long. It had a silver-tinged coat which was dark brown above, paler on the sides and nearly white ventrally. The muzzle was whitish and had many coarse whiskers.

Atkinson and Bryan note that the seals are fearless and readily handled, and Blackman (1941) says that if cornered they threaten the intruder by opening their mouths widely and uttering an abrupt barking noise. He also says that they do not migrate, and probably feed on squid and fish. Bailey notes that an animal collected by Henry Palmer in 1891 had its stomach full of half digested fish ; and he also makes an interesting observation that a large male seen in 1949 had a greenish-coloured face, but what the cause of this was he did not say.

SPECIMENS EXAMINED

The following specimens of *Monachus* have been examined. The list includes stuffed animals and skins, and unless otherwise mentioned the specimens are in the British Museum (Natural History).

M. monachus

Skulls only

1. 1853.10.6.4, 1063a. Presented by R. Macandrew.
   Deserta Grande Is. Madeira.
   Type of *Heliophoca atlantica* Gray, 1854.
   Skull and lower jaw of immature animal. Skull with the dorsal part of the cranium, interorbital and nasal regions missing.
   Stuffed animal also in the collection.
2. 1063b. Presented by R. Macandrew.
   Deserta Grande Is. Madeira.
   Skull incomplete—maxillary region bearing teeth, and fragmentary lower jaw only.
3. 1934.8.5.4 Collected by Barrett-Hamilton.
   Mediterranean.
   Complete skull and lower jaw.
4. 1951.4.17.1. From Rothschild Collection, Tring.
   Skull and lower jaw. Zygomatic arches broken.

Skulls and skeletons

1. 1063c. Presented by M. Verreaux.
   Algiers.
   Complete skull and skeleton of an immature animal.
2. 1863.4.1.1, 1421a. Male. Purchased from an Italian.
   N. Mediterranean.
   Complete skull and skeleton of an immature animal.
3. 1892.10.4.1, 1063d. Presented by C. F. R. Blandy.
   Deserta Grande Is. Madeira.
   Complete skull and skeleton of an immature animal.
4. 1892.11.7.1, 1063l. Presented by C. F. R. Blandy.
   Deserta Grande Is. Madeira.
   Complete skull and skeleton of very young animal.
   Skin also in collection.
5. 1894.7.27.1, 1063f. Male. Presented by C. F. R. Blandy.
   Deserta Grande Is. Madeira.
   Complete skull and skeleton of adult animal.
6. 1894.7.27.2, 1063g. Female. Presented by C. F. R. Blandy.
   Deserta Grande Is. Madeira.
   Complete skull and skeleton of adult animal.
   Skin also in collection.
7. 1894.7.27.3, 1063h. Male. Presented by C. F. R. Blandy.
   Deserta Grande Is. Madeira.
   Complete skull and skeleton of immature animal.

The seal was sent alive from Madeira and lived in the Zoological Gardens London from 16th July to 28th October, 1894.
Skin also in collection.

8. 1951.4.17.2. No history.
   Incomplete skeleton of an immature animal.
   No skull.

Skins

1. 1890.12.30.1. Male. Presented by H. C. Hinton and C. J. Cossart.
   Bugio, Deserta Grande Is. Madeira.
   Skin of an adult animal.
2. 1892.11.7.1, 1063l.
   Skin of very young animal noted above.
3. 1894.7.27.2, 1063g. Female.
   Skin of adult animal noted above.
4. 1894.7.27.3, 1063h. Male.
   Skin of immature animal noted above.

Stuffed animals

1. 1853.10.6.4, 1063a.
   Belonging to type of *H. atlantica* Gray, noted above.
2. 1910.9.27.1. Presented by Zoological Society of London.
   Presented to Zoological Society by Godfrey Williams.
   Madeira.
3. An immature animal with no history.

M. tropicalis

Skull only

1. 1889.11.5.1, 1064b. Male. Presented by F. D. Godman.
   Triangle Is. Gulf of Mexico.
   Collected in 1886 by Comision Geografico Exploradoro, Mexico.
   Skull and lower jaw of adult animal. Skull complete except for both jugals.
   Skin also in collection.

Skull and skeleton

1. 1887.8.5.1. Collected by H. L. Ward.
   Triangle Is. Gulf of Mexico.
   Complete skull and skeleton of adult, probably female animal.
2. K.7801, 899c. Presented by F. D. Godman.
   Triangle Is. Gulf of Mexico.
   Complete skull and skeleton of adult animal. In University Zoological Museum, Cambridge.

Skin

1. 1889.11.5.1, 1064b. Male.
   Skin of adult animal noted above.

Stuffed animal

1. 1847.2.2.2. Presented by P. H. Gosse.
   Jamaica.
   Type of *Phoca tropicalis* Gray, 1850.

M. schauinslandi

1. 32795.
   The skull of the type specimen collected on Laysan Id. by Dr. Schauinsland. The skull is in the Zoological Museum in Berlin and has not been examined, but photographs have been made available by Dr. K. Zimmermann, and a very complete set of measurements was published by Matschie (1905).
   A stuffed specimen is believed to be in the Bremen Museum.

OSTEOLOGY

A skull belonging to the genus *Monachus* has the following characters:

1. The skull is broad in proportion to its length.

2. The dorsal surface is convex, sloping backwards and forwards from a point about halfway along the interorbital region.

3. The interorbital region is broad and parallel-sided.

4. The naso-maxillary region is flattened dorsally.

5. The snout is broad, the sides of the maxillae being almost parallel from the upper edge of the infra-orbital foramen to the canines.

6. The molars are large and set more or less obliquely, and there are four upper and four lower incisors.

7. The condyle of the lower jaw is very low, on a level with a line drawn through the points of the molar teeth.

Comparison of the skulls of M. monachus, M. tropicalis *and* M. schauinslandi

1. In view of the small number of skulls examined, few general conclusions can be drawn from the measurements and proportions (Table I), although, as the following summary shows, skulls of *M. monachus* tend to be slightly wider in proportion to their length than skulls of *M. tropicalis* and *M. schauinslandi* (Text figs. 5 and 6, Pl. 6).

	M. monachus. %	*M. tropicalis.* %	*M. schauinslandi.* %
Zygomatic width	59·9–70·3	61·7–62·1	61·5
Snout width at canines	20·9–26·0	20·6–20·9	20·3
Width at external auditory meatus	53·1–58·5	49·8–50·5	50·5
Width at petrous bones	60·3–64·9	56·3–59·2	59·2

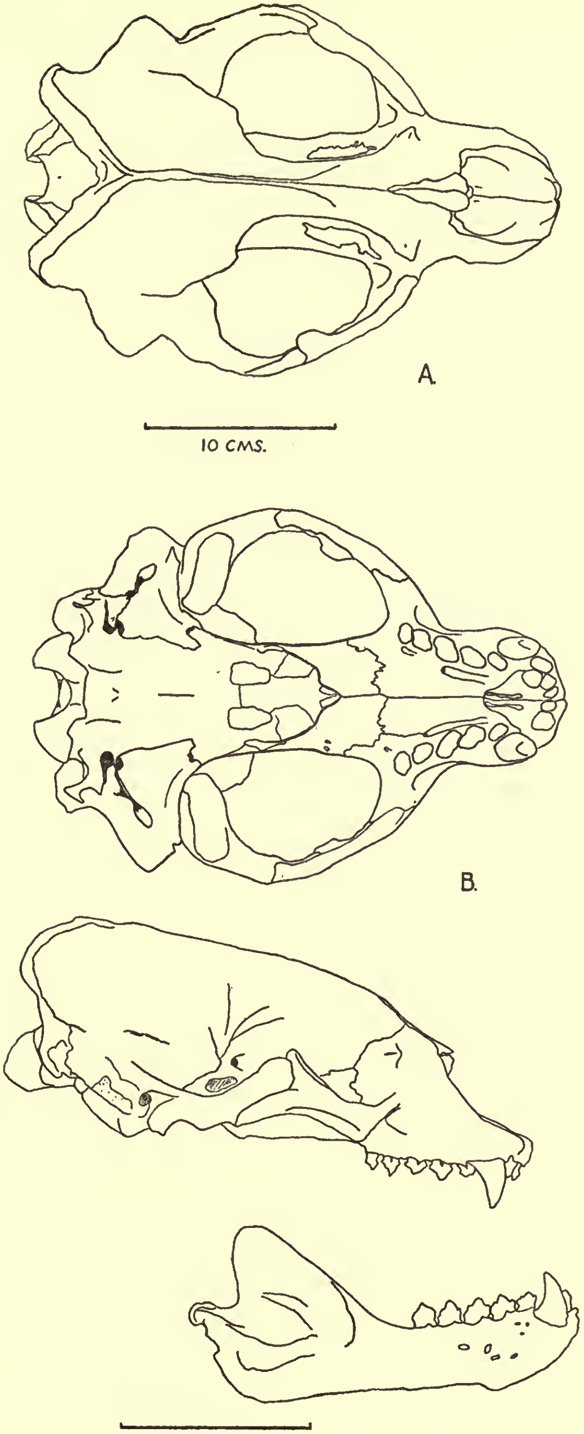

FIG. 5.—*M. monachus* Reg. No. 1894.7.27.1. A. Dorsal view of skull. B. Ventral view. Note supernumerary incisors. C. Lateral view of skull and lower jaw.

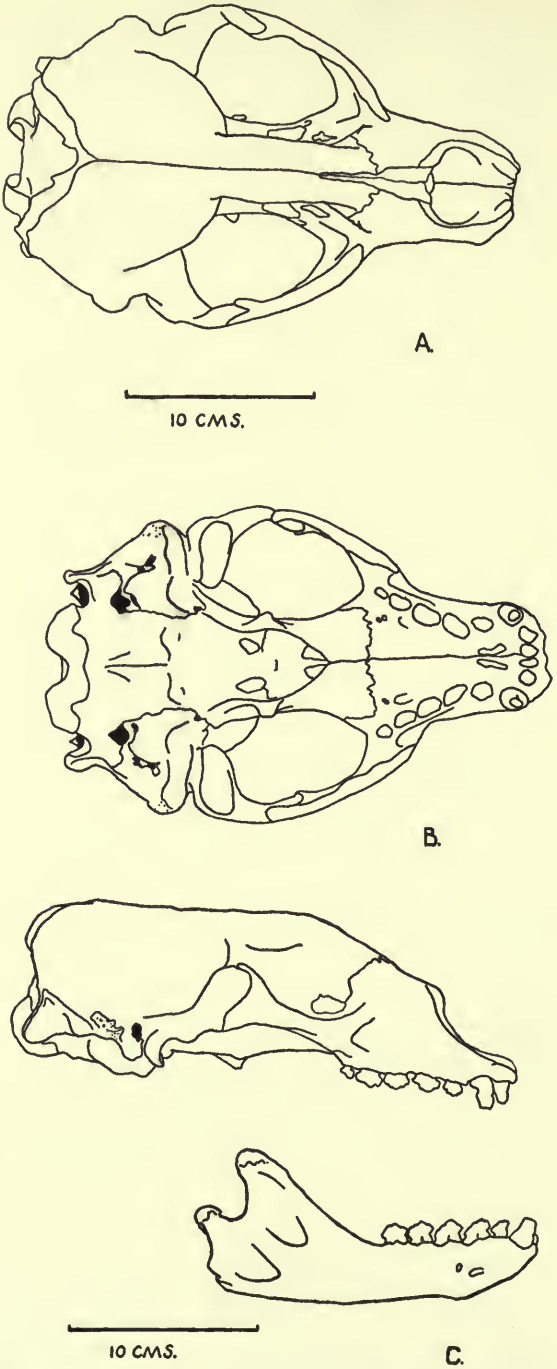
A.
10 CMS.
B.
10 CMS.
C.

Fig. 6.—*M. tropicalis* Reg. No. 1887.8.5.1. A. Dorsal view of skull. B. Ventral view. C. Lateral view of skull and lower jaw.

2. Each nasal of *M. monachus* ends anteriorly in a V, the point of the V, which may be slightly rounded, being directed anteriorly, so that the ends of both nasal bones together form a W. The nasal septum may project slightly beyond the nasal bones in old specimens. The nasal bones of *M. tropicalis* are much longer and narrower and their anterior ends continue the curve made by the premaxillae. The nasal septum forms a triangular projection. The nasal bones of *M. schauinslandi* are as long as those of *M. tropicalis*, but do not taper to so fine a point posteriorly. The anterior end of each has the form of an inverted V with the point directed posteriorly. The nasal septum appears to project a little beyond the end of the nasal bones (Text-fig. 7).

3. When seen from in front, the lower edge of the infraorbital foramen is wider than the upper edge in *M. monachus*, while the reverse is true in *M. tropicalis*. The foramen is not visible in the photographs of *M. schauinslandi*, although Matschie (1905) says that the lower edge is wider than the upper.

4. There is a well defined tubercle on the maxilla at the anterior margin of the orbit in *M. monachus*. This is very small and indistinct in *M. tropicalis*, and Matschie (1905) says that *M. schauinslandi* also has no clear tubercle in this position.

5. In *M. monachus* the zygomatic branch of the squamosal is not expanded at its anterior end and lies at an angle of approximately 45° with the base of the skull. The orbital process of the jugal is wide and upwardly directed while the lower branch is narrower and continues back along the squamosal for some distance.

In *M. tropicalis* the zygomatic branch of the squamosal is expanded at its anterior end and is much more nearly vertical. The orbital process of the jugal is very narrow and curves backwards over the top of the zygomatic branch, while its lower branch is short and triangular.

In *M. schauinslandi* the zygomatic branch of the squamosal is similar to that of *M. monachus*; it is not expanded and lies at an approximate angle of 45°. The orbital process of the jugal is not quite so wide as that of *M. monachus*, but is otherwise similar, and the lower branch is long and backwardly directed (Text-fig. 7).

6. The posterior end of the palate of *M. monachus* is U-shaped with a small median V-shaped incision. In *M. tropicalis* it is V-shaped, and in *M. schauinslandi* it forms a slightly wider V. (Text-fig. 7).

7. The pterygoid bones of *M. monachus* are low and ill-defined, and are not visible when the skull is viewed dorsally. In *M. tropicalis* they curve widely outwards and are visible dorsally. In *M. schauinslandi* they curve out as in *M. tropicalis*, but are not visible dorsally.

8. The coronoid process of the lower jaw of *M. monachus* is wide and concave internally. That of *M. tropicalis* is narrow and only very slightly concave. The coronoid of *M. schauinslandi* is narrow and like that of *M. tropicalis*.

9. From the above characters it will be seen that the skull of *M. schauinslandi* is more like that of *M. tropicalis* than *M. monachus*.

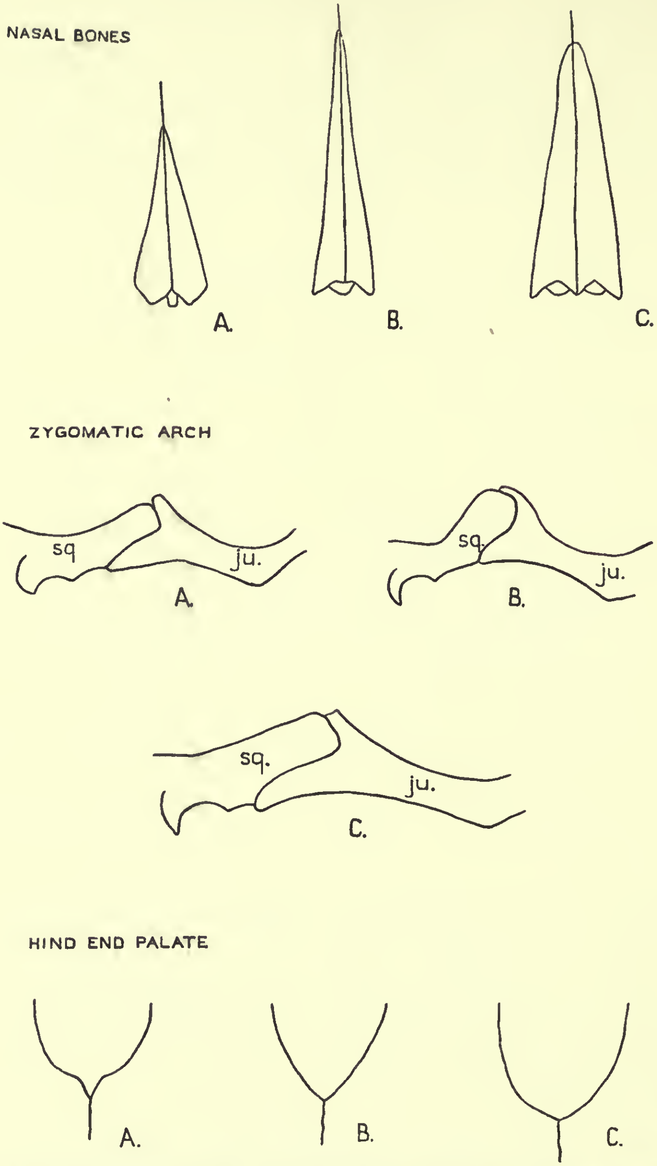
NASAL BONES
A.
B.
C.
ZYGOMATIC ARCH
sq
ju.
A.
sq.
ju.
B.
sq.
ju.
C.
HIND END PALATE
A.
B.
C.

FIG. 7.—Nasal bones, zygomatic arch and hind end of palate of A. *M. monachus*, B. *M. tropicalis*, C. *M. schauinslandi*. *sq.*, squamosal; *ju.*, jugal.

TABLE I.—*Cranial Measurements of* Monachus *Skulls.*

M. monachus.

	1951.4.17.1.		1894.7.27.1.		1863.4.1.1.		1894.7.27.2.		1934.8.5.4.	
	mm.	%	mm.	%	mm.	%	mm.	%	mm.	%
Condylobasal length	295	100	281	100	273	100	268	100	262	100
Condylo-basilar length	282	95·5	270	96·1	262	95·9	258	96.2	253	96·5
Basal length	279	94·5	263	93·5	251	91·9	251	93·6	241	91·9
Basilar length	266	90·1	252	89·6	241	88·2	241	89·9	232	88·5
Snout width at canines	71	24·1	68	24·1	71	26·0	57	21·2	55	20·9
Width of skull at front end of last upper molars	80	27·1	76	27·0	85	31·1	60	22·3	64	24·4
Zygomatic width	205 est.	69·4	193	68·6	185	70·3	176	65·6	159	60·6
Width at upper edge auditory meatus	166	56·2	156	55·5	150	54·9	145	54·1	139	53·1
Width at petrous bones	178	60·3	177	62·9	165	60·4	167	62·3	160	61·1
Palatal length	127	43·1	117	41·6	113	41·3	110	41·0	106	40·4
Palatilar length	113	38·3	107	38·1	103	37·7	100	37·3	97	37·0
Width of occipital condyles	65	22·0	67	23·8	64	23·4	65	24·2	65	24·8
Length of nasal suture	57	19·3	46	16·3	52	19·0	53	19·7	49	18·7
Length of upper molar row	64	21·6	60	21·3	64	23·4	57	21·2	56	21·3

M. monachus.

	1892.10.4.1.		1894.7.27.3.		1853.10.6.4.		1892.11.7.1.		1063c.	
	mm.	%	mm.	%	mm.	%	mm.	%	mm.	%
Condylobasal length	260	100	224	100	217	100	171	100	217	100
Condylo-basilar length	249	95·7	216	96·4	212	97·7	164	95·9	208	95·9
Basal length	241	92·6	207	92·4	197	90·8	156	91·2	197	90·8
Basilar length	230	88·4	198	88·4	191	88·0	147	85·9	188	86·6
Snout width at canines	61	23·4	52	23·2	51	23·5	44	25·7	50	23·0
Width of skull at front end of last upper molars	66	25·3	63	28·1	63	29·0	56	32·7	67	30·9
Zygomatic width	164	63·1	139	62·1	130	59·9	108	63·2	137	63·1
Width at upper edge auditory meatus	144	55·3	126	56·2	123	56·7	100	58·5	122	56·2
Width at petrous bones	163	62·6	138	61·6	136	62·7	111	64·9	136	62·7
Palatal length	102	39·2	90	40·1	91	41·9	73	42·7	92	42·4
Palatilar length	92	25·3	82	36·6	85	39·2	65	38·0	84	38·7
Width of occipital condyles	69	26·5	63	28·1	62	28·6	54	31·6	57	26·3
Length of nasal suture	48	18·4	53	23·6	—	—	38	22·2	39	17·9
Length of upper molar row	56	21·5	51	22·7	52	23·9	*ca*46	26·9	55	25·3

TABLE I—*cont.*

			M. tropicalis.				*M. schauinslandi.*	
	889c. (Cambridge)		1887.8.5.1.		1889.11.5.1.		32795.	
	mm.	%	mm.	%	mm.	%	mm.	%
Condylobasal length	272	100	269	100	267	100	265	100
Condylo-basilar length	263	96·7	262	97·3	258	96·6	255	96·2
Basal length	260	95·6	254	94·4	250	93·6	252	95·1
Basilar length	250	91·9	247	91·8	241	90·2	241	90·1
Snout width at canines	56	20·6	56	20·8	56	20·9	54	20·3
Width of skull at front end of last upper molars	77	28·3	74	27·5	80	29·9	70	26·4
Zygomatic width	168	61·8	167	62·1	165	61·7	163	61·5
Width at upper edge auditory meatus	136	50·0	136	50·5	133	49·8	134	50·5
Width at petrous bones	153	56·3	154	57·2	151	56·5	157	59·2
Palatal length	111	40·8	116	43·1	112	41·9	122	46·0
Palatilar length	102	37·5	110	40·8	104	38·9	112	42·2
Width of occipital condyles	67	24·6	69	25·6	63	23·5	66	24·9
Length of nasal suture	67	24·6	65	24·1	61	22·8	61	23·0
Length of upper molar row	66	24·3	65	24·1	66	24·7	—	—

M. monachus

Teeth

Dental formula: $i\frac{2}{2},\ c\frac{1}{1},\ m\frac{5}{5}$

Upper.—The incisors are large and pointed, the point directed posteriorly. The outer incisors are larger than the inner and there is a well developed cingulum on the inner surface of all four teeth.

The canines are of moderate size with a slight ridge down the posterior surface. The molars are large, the 3rd being the largest and the others decreasing in size in the order 3, 2, 4, 1, 5, except in the largest skull (1951.4.17.1) where the 5th is slightly greater than the first, and the others decrease in size from before backwards. Although the molars are set obliquely they do not overlap one another. The first molar makes an angle of 20° with the median palatal suture, the 2nd molar 40°, the 3rd molar 60°, the 4th molar 70° and the 5th molar 110°, so that its palatal surface is facing posteriorly. The external edge of the palate forms an angle of 20° with the median palatal suture. These measurements are from 1892.10.4.1, and are compared with a *Phoca vitulina* 1919.7.7.3260, where the teeth are set in line at an angle of 20°. There is a slight obliquity in the teeth of some of the other *P. vitulina* skulls, but this is not nearly so pronounced as in *M. monachus*. All the molars are double rooted except the first. The molars have a large central cusp and single smaller anterior and posterior cusps. The small cusps on the 5th molar are less distinct and the posterior one may be lacking. There is a well developed cingulum on the inner surface.

Variation.—In the nine specimens with fully erupted teeth, variations in the number of upper incisors occur in five of them.

1. 1853.10.6.4, 1063a.
   There is a small extra tooth just posterior to the first left incisor.
2. 1063b.
   Although the tooth is missing in the specimen, the alveolus shows evidence of an extra tooth posterior to the first right incisor.
3. 1894.7.27.1, 1063f.
   On the right side there is a small incisor median to the first and in the same line with it. The first incisor is the same size as that on the left side, though farther from the mid line. The second incisor on the right side is separated from the first by a gap, and leans away from it, towards the canine. It is considerably smaller than the left second incisor. Posteriorly and internally to the first and second right incisors is part of the root of a tooth larger than the left second incisor and smaller than the canine. The crown has been broken off since the animal died.
4. 1934.8.5.4.
   On the left side a small incisor is set directly behind the first.
5. 1951.4.17.1.
   On the left side a small incisor is situated just posteriorly to the first.

Disease.—Only one specimen shows any sign of disease in the teeth. 1863.4.1.1, 1421a—the second right incisor has lost most of the crown, the tooth is hollow, and there is some lumpy growth on its anterior surface. The parts of the premaxilla round the tooth have fallen away.

Lower.—The first incisors are considerably smaller than the second, they are set internally and posteriorly to them and are in a more or less recumbent position. They are similar to the upper incisors in shape ; the canines are also similar.

The third molar is the largest, the others decreasing in size in the order 3, 2, 4, 5, 1, so that the 1st molar is the smallest. The molars are set obliquely and do not overlap one another. The first molar is set directly behind the canine, so close that the two alveoli are confluent, but the molar is not on the inner surface of the canine as in the upper jaw. The angle the teeth make with the symphysial line is not so varied as in the upper jaw. The 1st molar makes an angle of 30°, the 2nd 40°, the 3rd 40°, the 4th 60°, and the 5th 20°. As the ramus itself is at an angle of 20° the 5th molar is in line with the jaw. These measurements are from 1863.4.1.1, 1421a. All the molars are double rooted except the first. The shape of the lower molars is similar to that of the upper, except that the posterior cusp on the 5th molar is generally present.

There are no variations in number, and no disease is present. The surface of all the teeth, both upper and lower, is slightly rugose.

M. tropicalis

Dental formula : $i\frac{2}{2},\quad c\frac{1}{1},\quad m\frac{5}{5}$

Upper.—The incisors are set in a straight line across the front of the premaxillae. They are similar in general shape to those of *M. monachus*, although there is more of a "waist" at the junction of root and crown. The canines are similar to those of *M. monachus*.

The molars are large, the 3rd is largest and the others decrease in size in the order 3, 2, 4, 1, 5. They are hardly oblique, the 2nd molar being the most so. The molars are double rooted except the first, and the last also appears to have only one root in the two British Museum specimens. The molars have a low central cusp, and one anterior and two posterior smaller cusps. The 5th molar has only a single posterior cusp. All the teeth have a well developed cingulum and the crown is slightly rugose.

Variation and disease.—In the three skulls examined there is no variation or disease in upper or lower teeth.

Lower.—The first lower incisors are smaller than the second, are set internally and posteriorly to them and are in a recumbent position. In shape they are similar to the upper incisors. The lower canines are similar to the upper ones.

The 3rd molar is the largest and the others decrease in size in the order 3, 4, 2, 5, 1, although molars 3, 4 and 2 are very much of the same size. The teeth are set in the line of the jaw, not obliquely. All the molars are double rooted except the first. The lower molars are similar in shape to the upper except that the cusps on the 1st are rather indistinct, and there is only one small posterior cusp on the 5th.

The teeth of *M. tropicalis* examined seem to be more worn than the teeth of *M. monachus*.

M. schauinslandi

Dental formula : $i\frac{2}{2},\quad c\frac{1}{1},\quad m\frac{5}{5}$

Upper.—The incisors are set in a straight line across the front of the premaxillae, and as far as can be seen from the photographs, the setting and shape of the teeth are similar to those of *M. tropicalis*. The molars are not set obliquely and seem to have a main low cusp, a single small anterior cusp and two small posterior cusps.

Lower.—The lower teeth appear to be similar to those of *M. tropicalis*.

Summary of the differences between the teeth

1. The incisors have a very pronounced "waist" at the junction of root and crown in *M. tropicalis* and *M. schauinslandi*.
2. The molars are set very obliquely in *M. monachus*.
3. The molars of *M. monachus* have a large central cusp and single smaller anterior and posterior cusps. Those of *M. tropicalis* and *M. schauinslandi* have a low central cusp, a single small anterior cusp and two small posterior cusps.

4. The incisors are set straight across the premaxillae in *M. tropicalis* and *M. schauinslandi*, but on a slight curve in *M. monachus*.

Teeth of a very young M. monachus

There is no exact information about the skull 1892.11.7.1, 1063l, but from its size and the condition of its teeth it is probably new-born. X-rays of the teeth were taken (Nos. 764 and 765) (Text-fig. 8).

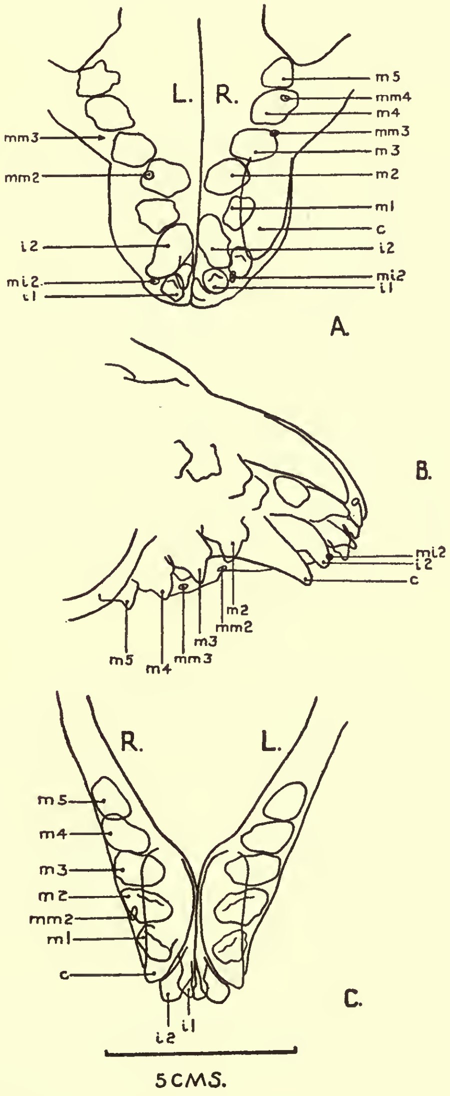
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FIG. 8.—Tracings from X-ray photographs of the teeth of a young *M. monachus*, Reg. No. 1892.11.7.1. A. Ventral view. B. Oblique view. C. Lower jaw.

Milk teeth

These are seen more clearly in the skull itself than in the X-ray. Six milk teeth are visible in the upper jaw, three on each side. They are very small, the largest being 2 mm. long; they have no roots and are present in the dried gum over the unerupted permanent teeth. The milk molars are placed behind their permanent successors. In the upper jaw milk molars 3 and 4 are present on the right side, and 2 and 3 on the left side. The two outer milk incisors are present. In the lower jaw the only milk tooth present is mm 2 on the right side.

There is no milk predecessor for the first molar in either upper or lower jaws.

Milk dentition: $i\frac{2}{2}$, $c\frac{1}{1}$, $m\frac{3}{3}$

Permanent teeth

The tips of all the permanent teeth are through the layer of dried skin on the skull, though probably apart from the upper canines, none of them would have pierced the gum in the living animal.

The permanent molars are large, but are normal in shape and position. This specimen shows an interesting variation in the number of incisors. The upper jaw has seven incisors, three of which are supernumerary. On the left side the outer incisor is in its normal position, the inner incisor is pushed a little further away from the mid line than is normal, and on its median surface, slightly posteriorly is a small extra tooth. On the right side the outer incisor is displaced posteriorly by an extra tooth which is between it and the canine, and between the inner incisor and the mid line is another extra tooth of the same size as the small extra one on the left side. The larger extra tooth on the right has the same size and appearance as the inner incisor.

The lower permanent teeth are normal.

Supernumerary bones in the skull.

Three of the youngest skulls of *M. monachus* (1892.11.7.1, 1063c and 1894.7.27.3) have supernumerary bones in the cranium. The youngest specimen (1892.11.7.1) has two bones symmetrically placed in the back of the skull, each bone bounded by exoccipital, parietal and supraoccipital. These bones are frequently found in the young of other seals and have been known as the tabulare, on the assumption that they were homologous with the tabulare of the reptilian skull. Doutt (1942) mentions their presence as well as that of two small adjacent bones, in skulls of *Phoca vitulina* and *P. hispida* and after quoting various authors who have considered the relationships of these bones with those in the reptilian skull, he thinks "that it is better, for the present at least, to consider these extra bones in the occipital region of the seal as being of the nature of fontanelle bones rather than to try to homologize them with elements in the reptilian skull". He says that these "extra-occipital" bones cannot be considered as Wormian bones for they are too symmetrical and too regularly situated.

Undoubted Wormian bones are also found in this skull and in the two other young ones mentioned. In 1892.11.7.1 they take the form of three small bones, two posteriorly and one anteriorly, at the junction of the two parietal bones with the frontal bones. In 1063c there is a single triangular bone in the same position. Also in the same position in 1894.7.27.3 there are two narrow bones one behind the other (Text-fig. 9).

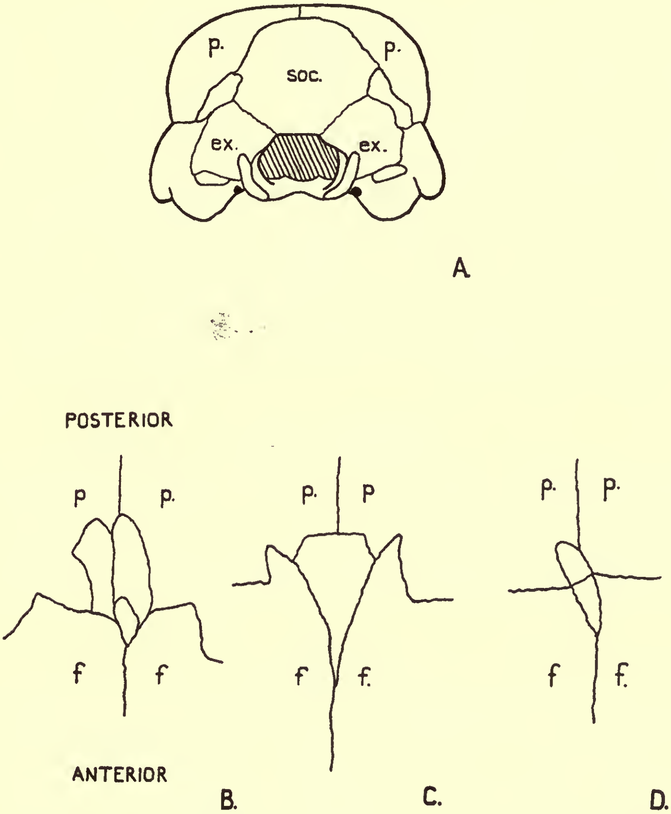

Fig. 9.—A. "Extra-occipital" bones in *M. monachus* Reg. No. 1892.11.7.1. B. Wormian bones in *M. monachus* Reg. No. 1892.11.7.1; C. Wormian bones in *M. monachus* Reg. No. 1063c; D. Wormian bones in *M. monachus* Reg. No. 1894.7.27.3. *p.*, Parietal; *f.*, frontal; *ex.*, exoccipital; *soc.*, supraoccipital.

Scapula (Text-fig. 10)

The scapula of *Monachus* is triangular in shape, the extreme antero-posterior length being greater than the height. In this character it differs from the scapulae of other Phocids where the anterior edge is much longer and, especially in the southern Phocids, much more square in shape. The junction of the posterior and dorsal edges is not hook-shaped. The spine is low and poorly developed like those of *Mirounga* and the southern Phocids, and very unlike the plate like spines of *P. vitulina* and *H. grypus*. The acromion process is well developed and resembles that of the southern Phocids, and the glenoid cavity is narrow and kidney-shaped. The outer surface of the scapula is convex anteriorly to the spine and concave posteriorly to it. Scapulae of *P. vitulina* and *H. grypus* are convex posteriorly and concave anteriorly.

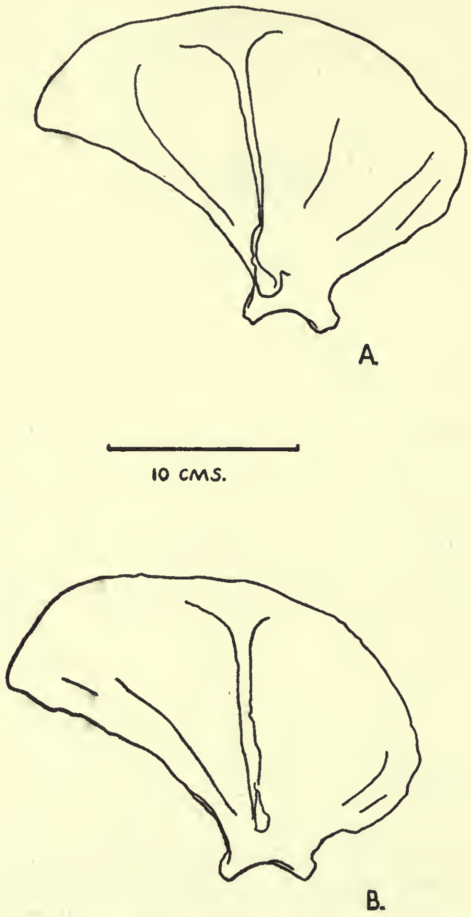

Fig. 10.—Scapulae of A. *M. monachus* Reg. No. 1894.7.27.1.
B. *M. tropicalis* 1887.8.5.1.

In young *M. monachus* and in *M. tropicalis* the anterior edge of the scapula sweeps round in a continuous curve from the neck, forwards and then back along the dorsal edge. In adult *M. monachus* the anterior edge is more squared off. The scapula of *M. tropicalis* is more elongated antero-posteriorly than that of *M. monachus*.

The separate origin of the coracoid is visible in three of the youngest specimens of *M. monachus*. In the youngest scapula (1892.11.7.1) it does not appear to have begun to ossify. Scapulae 1894.7.27.3, and 1063c have the cartilage still present over the glenoid cavity and the coracoid is visible as a distinct bone embedded in it. Scapula 1892.10.4.1 has no cartilage, the coracoid has fused to the anterior edge of the glenoid cavity, but is still recognizable as a separate entity.

Humerus

The humerus is short and robust. In common with all the southern Phocids there is no supracondylar foramen. This foramen is present in *Phoca, H. grypus, E. barbatus* and *C. cristatus.* The deltoid ridge is strongly developed and extends nearly the whole length of the shaft. The deltoid rugosity on the external surface of the ridge is more prominent in *M. monachus* than in *M. tropicalis,* but does not overhang to so great an extent as in *Phoca, Halichoerus* and *Erignathus.* The bicipital groove is broad and shallow. In *Monachus* and the southern Phocids there is only a very poorly marked supinator ridge, while this is well developed in the northern Phocids. For bones of approximately the same length, the humerus of *M. tropicalis* (Pl. 7,A) is slightly more slender than that of *M. monachus.* The distal articular surface is narrower and appears to be slightly more oblique than in *M. monachus.* In *M. tropicalis,* but not in *M. monachus* there is a very slight anconeal fossa.

Radius and Ulna.

The radius is laterally flattened and bowed forward, so that its hinder edge is concave. The ulna is compressed laterally, with an expanded olecranon process and a concave hinder margin. The ulna of *M. monachus* is slighty more stoutly built than that of *M. tropicalis,* but presents no special modifications.

Manus (Pl. 7,A)

The carpus consists of seven bones: scapholunar, trapezium, trapezioid, os magnus, unciform, cuneiform and pisiform. The length of the digits, and of the metacarpals decreases in size from the first to the fifth. The first digit is strongly built, the fifth slightly less so, and the second, third and fourth of equal thickness. The terminal phalanges are grooved for the insertion of claws. An X-ray taken of the manus of an immature *M. monachus* (1894.7.27.3) shows the presence of distal epiphyses on all five metacarpals, but a proximal epiphysis on only the first. All the phalanges except the terminal ones have epiphyses on both ends, and a proximal epiphysis is visible only on the first terminal phalange, it not yet having ossified on the remaining phalanges.

Pelvis and sacrum

The innominate bones are of the typical Phocid pattern with short recurved ilia and long ischia and pubes. The symphysial area is very small and appears to be mainly cartilaginous. The innominate bones of *M. monachus* have thick flattened ilia which are not excavated on their exterior surfaces as in *Phoca* and *Halichoerus.*

When compared with the innominate bones of other Phocids it is seen that the ilia of *M. monachus* are everted and also are rotated upwards relative to the plane of the pubes and ischia, so that the external surfaces of the ilia face slightly posteriorly and dorsally. In *Phoca* and *Halichoerus* and also in the southern Phocids the ilia are everted in approximately the same plane as the pubes and ischia. The ischium of *M. monachus* is strongly built, approximately circular in cross section until about the level of the ischiatic spine, when it continues as a flat bar. The pubis is also thicker at its origin and flattens out posteriorly to meet the ischium. The ischium forms the upper and practically the whole of the posterior border of the obturator foramen before it meets the pubis.

A comparision of the innominate bones of Phocids shows that in the northern genera *Phoca*, *Halichoerus* and *Erignathus* the obturator foramen is long and narrow and the width of the innominate at the level of the ischiatic spine less; in the southern genera *Ommatophoca*, *Hydrurga*, *Leptonychotes*, *Lobodon* and *Mirounga* the obturator foramen is broad and the width of the innominate correspondingly greater. The proportions of the obturator foramen given in the table below indicate a closer relationship of *Monachus* with the Southern than the Northern Phocids (Pl. 8).

Measurements of the Obturator Foramen

	Extreme antero-posterior length. (mm.)	Greatest width. (mm.)	Proportion of width to length.
P. vitulina	96	31	32·3
H. grypus	100	26	26·0
E. barbatus	112	37	33·0
L. weddelli	103	43	41·7
H. leptonyx	107	57	53·3
L. carcinophagus	97	53	54·6
O. rossi	88	45	51·1
M. monachus			
1063g.	94	51	54·3
1063f.	98	55	56·1
1421a.	82	50	60·9
M. tropicalis			
1887.8.5.1	112	50	44·6
899c.	114	52	45·6

In *M. monachus* the pectineal tubercle and the ischiatic spine are well developed, the acetabulum is deep and circular with a well marked cotyloid notch. The innominate bones articulate with two sacral vertebrae, but in the three adult *M. monachus*, two have four vertebrae fused to form the sacrum, and one—the youngest—has three. The wings of the sacrum are broad and strong, and articulate on their posterior surfaces with the ilia.

In most respects the pelvis of *M. tropicalis* is similar to that of *M. monachus*, but the size of the ischium and pubis differs considerably. The pubis is extremely strongly built, is circular in cross section, tapers slightly towards its posterior end and does not flatten out except at the symphysial area. The ischium is much more slender than the pubis, and posterior to the ischiatic spine it is only a very narrow bar, triangular in cross section.

Femur

The femur is short and flattened antero-posteriorly. The greater trochanter is large and thickened and is separated from the head by a groove which is deeper and more distinct in *M. monachus* than in *M. tropicalis*. In common with all Phocids except *Phoca* and *Halichoerus* there is no trace of a digital fossa. The distal end of the femur is very broad because of the great development of the epicondyles. In general shape, and in particular in the great width in proportion to its length, the femur of *Monachus* is more like that of the Southern than the Northern Phocids.

Patella

The patella of *M. monachus* is a small flat bone articulating with the femur. The measurements of specimen 1033f are: Greatest antero-posterior length 26 mm. Greatest height anteriorly 15 mm. The patella of *M. tropicalis*, while of the same general length, is, particularly in the Cambridge specimen, higher and more pyramidal. The measurements of the British Museum and Cambridge specimens respectively are: Greatest antero-posterior length 30 mm., 24 mm. Greatest height anteriorly 20 mm., 28 mm.

Tibia and Fibula

The tibia and fibula are of the usual pinniped form, the two bones being fused at the proximal end, but separate from each other at the distal end. In only one of the *M. monachus* in the collection (1063g) is one of the fibulae fused to the tibia, so this fusion must be one of the last to occur. The posterior tibial fossa is less concave than in any of the other Phocids examined, but the tibial spine and the anterior tibial fossa are quite well marked. Both the tibia and the fibula articulate at their lower ends with the astragalus.

Pes (Pl. 7,B)

The tarsus consists of seven bones: astragalus, calcaneum, navicular, cuboid and external, middle and internal cuneiform bones. The length of the digits and of the metacarpals decrease in size in the order 1, 5, 2, 4, 3, the middle digit being the shortest. The outer digits are the most strongly built. The terminal phalanges are grooved for the insertion of small claws. An X-ray taken of the pes of a young *M. monachus* (1894.7.27.3) shows the presence of distal epiphyses on all the metatarsals, and a proximal one on the first only. Epiphyses are visible on both ends of all the phalanges except the terminal ones. Epiphyses have not yet ossified on the proximal ends of any of the terminal phalanges except the first.

Vertebral Column

The vertebral formula is as follows:

	Cervical.	Thoracic.	Lumbar.	Sacral.	Caudal.
M. monachus					
1892.11.7.1, 1063l.	7	15	5	2	3+
1894.7.23.3, 1063h.	7	15	5	3	11
1894.7.27.2, 1063g.	7	15	5	4	11
1894.7.27.1, 1063f	7	15	5	4	11
1892.10.4.1, 1063d	7	15	5	3	11
1863.4.1.1, 1421a	7	15	5	3	11
1063c	7	15	5	2	10
M. tropicalis					
1887.8.5.1	7	15	5	3	12
899c	7	15	5	3	12

Cervical vertebrae

M. monachus.—The centra are approximately circular in cross section and the ventral surfaces have a median keel in all except the atlas. The neural arches are narrow antero-posteriorly, the widest (the 7th) being 20 mm., and the neural spines increase from a hardly perceptible point on the third vertebra to a spine 38 mm. high on the seventh. The transverse processes are perforated by the vertebrarterial canal in all except the seventh. The transverse processes of cervical vertebrae 3–6 inclusive are, in all the Phocidae examined, divided into two branches, a dorsal transverse element which is more or less at right angles to the median plane, and directed slightly posteriorly, and a ventral costal element which is directed more or less vertically downwards and is expanded antero-posteriorly into a plate which is greatest in the sixth vertebra. In *M. monachus* the transverse processes leave the centrum at an angle of approximately 45° and are not divided into two branches (Text-fig. 11).

The cervical vertebrae of *M. tropicalis*, while conforming to the same general pattern as those of *M. monachus*, are different in several minor respects. They give the general impression of being more finely built than those of *M. monachus*. The transverse process of the atlas is not so massive and the vertebrarterial canal is much larger, the neural spine of the axis is not so high and does not project so far backwards. The transverse process of the axis is thin and pointed, those of vertebrae 3–6 are divided into two branches, the costal element not being so expanded as in *Phoca* and directed not vertically, but laterally at an angle of approximately 45°, and inclining posteriorly. The general shape of the cervical vertebrae and in particular that of the transverse process is more like *Leptonychotes* than *Phoca*.

It is interesting to note that both in the British Museum and the Cambridge specimens of *M. tropicalis* the neural arches of the third and fourth vertebrae do not meet dorsally. In the British Museum specimen the two sides of the neural arch of the fifth vertebra are fused, but the lateral tips of the spine are curved outwards, to give a bifurcated tip to the spine. The lateral tips of the sixth spine are less curved. In the Cambridge specimen the two sides of the fifth neural arch meet, but are not fused, and the tips curve outwards. The spine of the sixth is fused with curved tips, and the spine of the seventh in both animals is normal. A similar non-fusion of the neural arch occurs in *M. monachus* 1063c, where the two sides of the third neural arch fail to meet. The remaining arches are normal and do not have the bifurcated appearance of those of *M. tropicalis*. Ward (1887b)

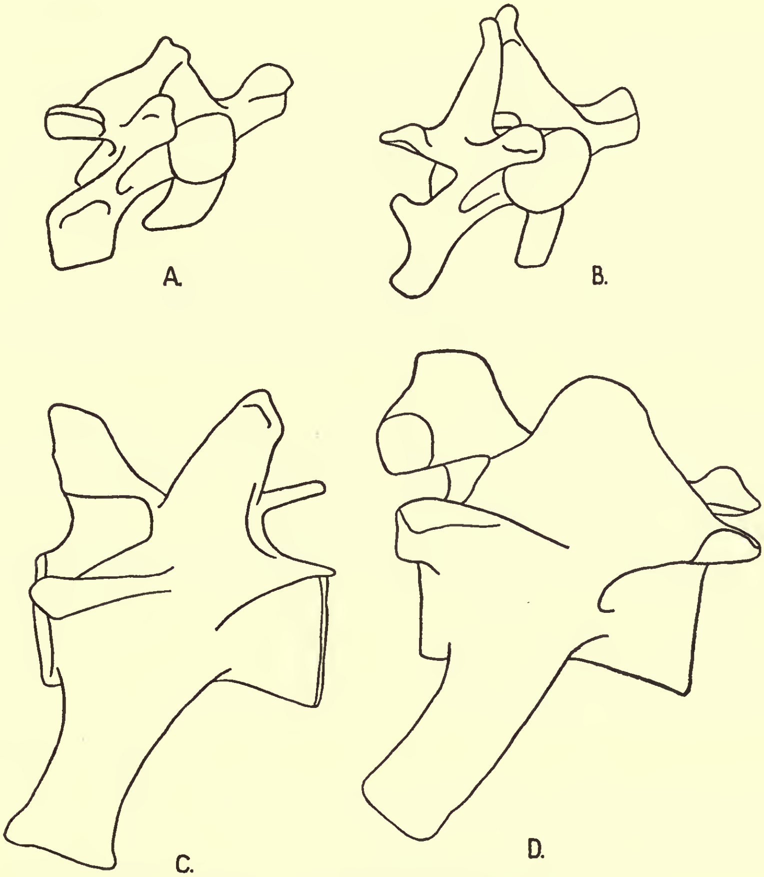

FIG. 11.—A. 5th cervical vertebra of *M. monachus* Reg. No. 1894.7.27.2. B. 5th cervical vertebra of *M. tropicalis* Reg. No. 1887.8.5.1. C. 2nd lumbar vertebra of *M. monachus* Reg. No. 1894.7.27.2. D. 2nd lumbar vertebra of *M. tropicalis* Reg. No. 1887.8.5.1.

says, describing *M. tropicalis,* " At no time does this seal raise its head as much above the line of its back as does the harbor seal: the flexibility of its cervical vertebrae appearing to be quite restricted ". It is difficult to know whether this is a character that applies to *M. tropicalis* in general, or only to the animals that Ward saw; or whether it has any connection with the non-fusion of the neural spines, as the two animals in which this character is present were both collected by Ward from a single group of animals.

Thoracic vertebrae

The thoracic vertebrae of *M. monachus* articulate with fifteen pairs of ribs. Ribs 1 and 2, and 11, 12, 13, 14 and 15 articulate only with the corresponding thoracic vertebra, but the capitular articulation of ribs 3–10 inclusive overlaps on to the centrum of the vertebra in front. Ribs 1–13 inclusive articulate by both capitular and tubercular heads, the two articulations getting closer together until ribs 14 and 15 articulate by means of a single head only. The transverse processes are prominent, but diminish in size from the first to the tenth vertebra and are hardly visible from the eleventh to the fifteenth. The neural spines are high and pointed in the first five vertebrae, but get progressively smaller and more backwardly inclined.

Between thoracic vertebrae 9 and 10 in specimen 1863.4.1.1, the anterior common ligament has ossified in the form of a bony plate, which is fused to the centrum of the tenth vertebra and extends anteriorly for 4cm. beyond it. Evidences of a similar abnormality, though to a much lesser extent, are present on the ventral surfaces of the centra of vertebrae 11, 12 and 13.

The thoracic vertebrae of *M. tropicalis* are practically the same as those of *M. monachus* except that the neural arches are wider and the neural spines are shorter and less pointed.

Measurements of thoracic vertebrae

	M. monachus. 1063g. mm.	*M. tropicalis.* 1887.8.5.1. mm.
Length medially of neural arch of 10th vertebra	48	46
Least width ,, ,, ,,	25	34
Height* of neural spine of 1st vertebra	58	51
,, ,, ,, 5th ,,	65	52
,, ,, ,, 10th ,,	54	46
Length of centrum of 1st ,,	41	40
,, ,, ,, ,, 10th ,,	52	51

* Height not taken vertically, but medially along spine.

Lumbar vertebrae

The lumbar vertebrae of *M. monachus* have large heavy centra that are slightly concave ventrally. The transverse processes are prominent and project anteriorly and ventrally. The cephalic articular processes are large and are directed obliquely anteriorly, but the caudal articular processes are extremely small and thin, and may not even reach the vertebra behind. The neural spines are stoutly built and are directed slightly posteriorly.

The right transverse process of the first lumbar vertebra of *M. monachus* 1063f is normal, but the left is stout, truncated, and its distal end forms an articulation for a small triangular " pleurapophysial " ossicle 34 mm. in length.

A condition of chronic osteo-arthritis is present on the posterior half of the centrum of the fifth lumbar vertebra of *M. monachus* 1063g, and this condition has spread to the centrum of the first sacral vertebra.

The lumbar vertebrae of *M. tropicalis* are in general like those of *M. monachus*, though the articulations are normal, the caudal articular process overlapping to a considerable extent the cephalic articular surface of the next posterior vertebra. The neural spines are laterally flattened, low, rounded, and either vertical or inclined slightly anteriorly (Text-fig. 11).

Caudal vertebrae

Except for the first two or three, the caudal vertebrae are without a neural arch, and both the number and size of the processes, and also the size of the centrum, diminish in size from before backwards.

Ribs

The articulations of the ribs with the thoracic vertebrae have already been discussed. In *M. monachus* (1063f) the ribs increase in length from the 1st (77 mm.) to the 11th (263 mm.) and then decrease to the 15th (209 mm.). In *M. tropicalis* (1887.8.5.1) similar measurements are 1st (71 mm.), 11th (255 mm.) and 15th (189 mm.).

The adult specimens of *M. monachus* in the collection lack the cartilaginous portions of the ribs. An immature *M. monachus* (1063c) has cartilaginous ribs attached directly to the sternum from bony ribs 1–9 inclusive. Cartilaginous ribs 10–15 inclusive turn forward and lie against the cartilaginous portion of the rib in front.

Cartilaginous ribs 1–10 inclusive of *M. tropicalis* (1887.8.5.1) are attached directly to the sternum, 11 and 12 are long and lie against the cartilaginous portion of the ribs in front, but the cartilaginous portions of ribs 13–15 are very short, between 35 and 70 mm. long, and are unattached ventrally.

The first cartilaginous rib articulates with the manubrium of the sternum, the remaining nine with the cartilages between the sternebrae, ribs both 8 and 9 articulating with the last cartilage.

Sternum

The sternum of both *M. monachus* and *M. tropicalis* consists of nine sternebrae, although there are only eight present in *M. monachus* 1063c. The sternebrae are dorso-ventrally flattened and more or less quadrate in shape, the first and last being more elongated. The xiphisternum is prolonged posteriorly into two cartilaginous extensions, the ends of which are expanded and joined together posteriorly.

GROWTH

In view of the small number of specimens available no attempt at age determination has been made but it has been possible to do a certain amount on the growth of the skull and skeleton.

Following Doutt's (1942) method for estimating the " suture age " of the skull the following table was drawn up. (Table II). As suture closure is a gradual process the degree of closure has been given a value : 1 for open, 2 for less than half closed, 3 for more than half closed, and 4 for completely closed, and the total for each skull is known as the " suture age " for that specimen.

TABLE II.—*Suture Ages of the Skulls*

Registered No.	Occipito-parietal.	Squamoso-parietal.	Sagittal.	Coronal.	Basioccipito-basisphenoid.	Basisphenoid-presphenoid.	Interfrontal.	Intermaxillary.	Fronto-maxillary.	Jugal-maxilla.	Squamosal-jugal.	Palato-maxillary.	Suture age.	Condylo-basal length, mm.
M. monachus :														
1892.11.7.1	1	1	1	1	1	1	1	1	1	1	1	1	12	171
1063c	1	1	1	1	1	1	1	1	1	1	1	1	12	217
1894.7.27.3 ♂	2	1	1	1	1	1	1	1	1	1	1	1	13	224
1892.10.4.1	4	1	1	2	1	1	1	1	1	1	1	1	16	260
1934.8.5.4	4	1	2	2	2	1	1	1	1	1	1	1	18	262
1894.7.27.2 ♀	4	4	4	4	4	4	1	1	1	1	1	1	30	268
1863.4.1.1 ♂	4	4	4	3	4	1	1	1	1	1	1	1	26	273
1894.7.27.1 ♂	4	4	4	4	4	2	1	1	1	1	1	1	28	281
1951.4.17.1	4	4	4	4	4	4	1	1	1	1	—	1	29+	295
M. tropicalis :														
1889.11.5.1	4	4	4	2	4	1	1	1	1	1	1	1	25	267
1887.8.5.1	4	4	4	3	4	4	1	3	1	3	1	1	33	269

The order of suture closure is as follows :

1. Exoccipital—basioccipital.
2. Occipito—parietal.
3. Squamoso—parietal
Sagittal.
Coronal.
Basioccipito—basisphenoid.
7. Basisphenoid—presphenoid.

In Table II the skulls are placed in order of condylo-basal length, and it can be seen that the one known female skull of *M. monachus* has a higher " suture age " in proportion to its condylo-basal length than the other skulls, i.e. it matures at a smaller size. For this reason it seems likely that the skull and skeleton of *M. tropicalis* 1887.8.5.1 are also from a female.

Table II also shows that the series of skulls of *M. monachus*, although more or less uniformly distributed over a size range, is divisible by " suture age " into two discontinuous groups—those with " suture ages " 12–18 and those from 26–30.

This is clearly shown in the table of percentage increases below, from which it is also evident that while the " suture age " increases from 12–18, an increase of six units, there is a general increase in the size of all the components of the skull, the average amount being 53% or 9% per unit of " age ". During the period when the " suture age " increases by four units from 26 to 30 there is also an increase in all the components with one exception, but the average rate of increase per unit of " age " is now only 4.5%. A diminution in the rate of increase with age is to be expected, but one component—the cranium—appears virtually to have ceased growing by the time a " suture age " of 18 is reached ; there are no crania in the 26–30 group larger than the largest individuals in the 12–18 group.

		Percentage increases.					
" Suture age."	Condylo-basal length, mm.	Cranium length.	Inter-orbital length.	Snout length.	Width at canines.	Zygomatic width.	Width at external auditory meatus.
12–18	171–262	46	77	59	39	52	44
19–25	—	Negative	13	8	Negative	7	0·7
26–30	268–295	2	11	24	25	17	15

The most striking feature of the above table is that, despite the absence of any large size discontinuity in the series, there is a complete absence of any specimen in the large " suture " group 19–25 ; the largest specimens of the " younger " 12–18 group are almost as large as, and in some components larger than the smallest individuals of the " older " 26–30 group.

It is not likely that growth proceeds in this erratic fashion and therefore it is concluded that the " suture age " is not a rectilinear age index. It seems clear that at a certain stage of growth there is a very rapid suture closure. After this stage is past the skull components continue growing with the notable exception of the cranium. Skulls with a condylo-basal length of less than ± 265 mm. have a rapidly growing cranium and during this growth-phase the occipito-parietal, sagittal, coronal and basioccipito-basisphenoid sutures are closing. At ± 265 mm. condylo-basal length there is rapid suture closure affecting the occipito-parietal, squamoso-parietal, sagittal, coronal, basioccipito-basisphenoid and basisphenoid-presphenoid sutures, and cranial growth ceases. After this, growth of the facial elements continues and the interfrontal, intermaxillary, fronto-maxilla, jugal-maxilla, squamosal-jugal and palato-maxilla sutures are open in all the skulls of *M. monachus* in the collection.

It is possible that the " suture age " figures give an approximation to a rectilinear age index if the 19–25 period is eliminated, and if this is done the relative " ages " of the skulls are 12 : 12 : 13 : 16 : 18 : 23 : 19 : 21 : 23. The "suture age" 12 includes two skulls which are both young but which are clearly at very different stages of growth. The youngest skull—1892.11.7.1—has not been included in the graph as it is so much younger than its "suture age" indicates, this criterion being invalid for very young (and probably very old) skulls.

Plotting the skull measurements against this time scale (Text-fig. 12) gives a

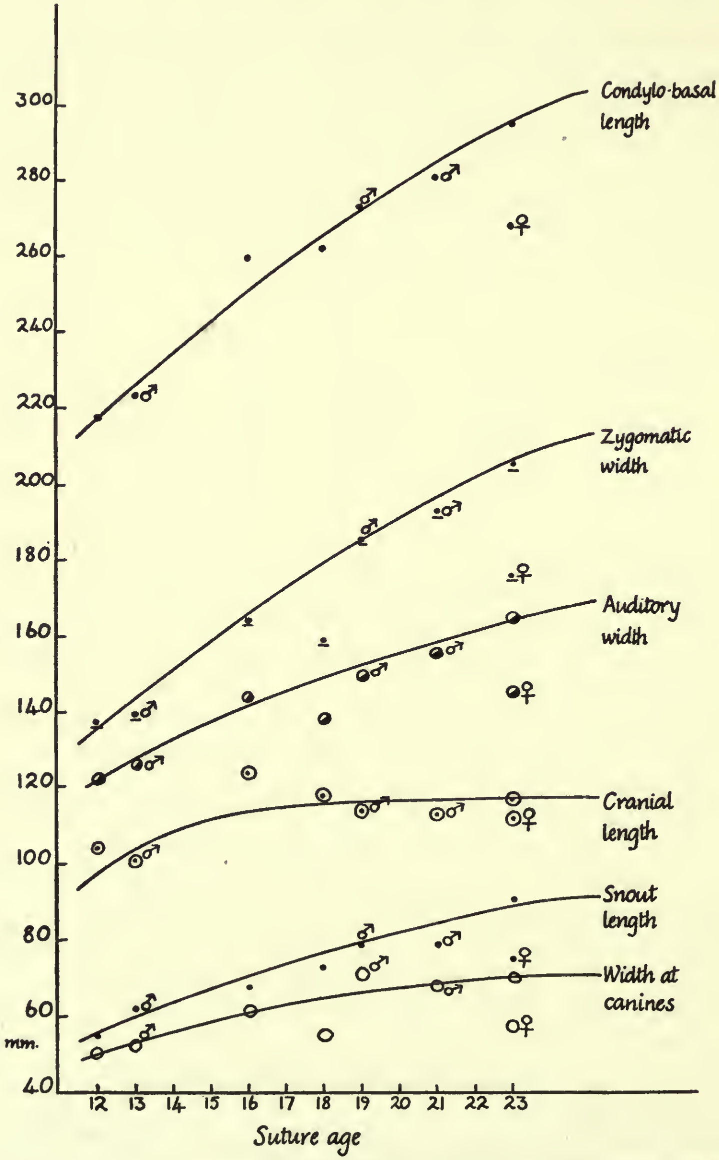

FIG. 12.—Graph showing relative growth rates of different regions of the skull.

picture which is not an unreasonable one, and one which suggests certain sex differences. Even if the time scale is only an approximation, plotting all the bones to this scale gives a series of curves that are directly comparable. The slope and shape of these curves show the relative growth rates and growth patterns of the different elements.

From a visual inspection of a series of skulls of *M. monachus* of ascending size, it is obvious that the various regions of the skull do not all grow at the same rate. The cranium for instance, while it increases in length, does not do so nearly so quickly as the facial region. Measurements of the cranial, interorbital and snout regions were taken between uprights and these, together with width measurements are seen in Table III. The interorbital region is measured to the maxillary tubercle at the anterior edge of the orbit.

The logarithmic values of the various measurements were plotted in turn against the logarithmic value of the condylo-basal length. The points fall approximately about a straight line, showing that there is allometric growth. This being so, it may be taken that the rates of growth of the various parts of the skull relative to the condylo-basal length satisfy the equation $y=bx^k$, where x is the condylo-basal length, y the length of the part, b the fractional coefficient (the value of y when $x=1$) and k the growth coefficient.

TABLE III

Registered No.	Condylo-basal length. mm.	Cranium length. mm.	Inter-orbital length. mm.	Snout length. mm.	Snout width at canines. mm.	Zygo-matic width. mm.	Width at upper edge external auditory meatus. mm.
M. monachus							
1892.11.7.1	171	85	40	46	44	108	100
1063c	217	104	58	55	50	137	122
1894.7.27.3	224	101	61	62	52	139	126
1892.10.4.1	260	124	68	68	61	164	144
1934.8.5.4	262	118	71	73	55	159	139
1894.7.27.2	268	112	81	75	57	176	145
1863.4.1.1	273	114	80	79	71	185	150
1894.7.27.1	281	113	89	79	68	193	156
1951.4.17.1	295	117	87	91	71	205	166

The growth coefficient is the tangent of the angle between the horizontal and the line joining the points. Values of *k* greater than unity indicate an increasing rate of relative growth, and those less than unity the converse. The following are the values of *k* for the various parts :

Cranium length	0·62
Interorbital length	1·81
Snout length	1·32
Snout width	0·95
Zygomatic width	1·15
Auditory meatus width	0·85

These figures bear out the visual evidence as they show that the interorbital and snout regions, and the zygomatic width have a much faster relative growth than the rest of the skull, while the cranium, the snout width and the width of the cranium between the external auditory meatuses grow at a much slower rate.

Although fusion of the bones of the skull commences at an early age, the epiphyses of the skeleton do not fuse until comparatively late. The following is the order of fusion of the epiphyses and skeletal elements :

1. Pelvic elements.
2. Sacral vertebrae.
Humerus (distal).
Femur (proximal).
5. Vertebral epiphyses.
Humerus (proximal).
Radius (proximal).
Femur (distal).
Tibia (proximal).
Fibula (proximal).
11. Ulna (proximal).
Metacarpal epiphyses.
Metatarsal epiphyses.
14. Fibula to tibia.
15. Radius (distal).
Ulna (distal).
Tibia (distal).
Fibula (both epiphyses).
} Not fused in any specimen in collection.

The above list shows that the epiphyses of the limb bones tend to fuse first to the bones nearest the body—humerus and femur—and the fusion proceeds outwards to the digits. In the youngest animal (1892.11.7.1) the separate elements of the vertebrae have not yet fused, and the fusion of the vertebral epiphyses to the centra in the older animals appears to start at the cervical end of the column and proceed caudally.

In order to see how the limb bones and pelvis increase in length with age, measurements were taken of the lengths of the pelvis and of the shafts of five limb bones, not including the epiphyses, of three male animals of increasing age, and the new-born specimen, as there can be no difference due to sex at this age. There are, unavoidably, many inaccuracies in the table (Table IV). The shaft length is difficult to measure exactly in the two youngest animals because of the large amount of cartilage present where the epiphyses are not fully ossified. The proportions, using the measurements of the largest specimens as 100%, are taken on the assumption that all the animals will grow to this size. This is obviously not so, and even this animal is not fully mature, but it is the oldest that is known to be male. The table shows that the pelvis has over half (62.2%) of its growth in length to complete after the animal is born. The corresponding figures for the limb bones are: humerus 45.4%, radius 50%, femur 54.3%, and tibia 55.4%.

Table IV

Registered No.	Humerus.		Radius.		Femur.		Tibia.		Pelvis.	
	mm.	%	mm.	%	mm.	%	mm.	%	mm.	%
M. monachus :										
1892.11.7.1	59	54·6	63	50·0	43	45·7	91	44·6	92	37·8
1894.7.27.3 ♂	76	70·0	80	65·1	58	61·7	127	62·2	147	60·4
1863.4.1.1 ♂	101	93·5	118	93·6	88	93·6	186	91·1	221	90·9
1894.7.27.1 ♂	108	100	126	100	94	100	204	100	243	100

RELATIONSHIPS OF THE GENUS *MONACHUS* FLEMING 1822

Family Phocidae Gray, 1825.

Subfamily Monachinae Trouessart, 1904.

The Phocidae are divided into the subfamilies Phocinae, including *Phoca, Erignathus* and *Halichoerus*, with the incisive formula $\frac{3}{2}$; the Cystophorinae including *Cystophora* and *Mirounga*, with incisors $\frac{2}{1}$; the Lobodontinae, including *Lobodon, Hydrurga, Leptonychotes*, and *Ommatophoca* with incisors $\frac{2}{2}$; and the Monachinae with the single genus *Monachus* also with incisors $\frac{2}{2}$.

The Cystophorinae are quite distinct, and are not considered here. Some of the characters which distinguish the Phocinae from the Lobodontinae are: the zygomatic process of the maxilla with the posterior border subvertical, not extending far backwards beneath the malar; nails of all the digits well developed; and the outer digits of the pes not much prolonged beyond the others. In the Lobodontinae the zygomatic process of the maxilla is prolonged backwards beneath the malar; the nails of the hind limbs rudimentary; and the outer digits lengthened.

A comparison of members of the genus *Monachus* with members of the two preceding subfamilies shows that in the skull the incisive formula is the same as in the Lobodontinae, the extension backwards of the zygomatic process of the maxilla is not quite so great as in the latter subfamily, but is very much greater than in the Phocinae. All members of the Phocinae have large claws on both fore and hind flippers, while *Monachus* agrees with the Lobodontinae in having the hind claws very much reduced. A further similarity is in the shape of the hind flippers which have the two outer digits very much longer than the inner ones, the first digit of the fore flippers is the longest and the rest get gradually shorter. In the Phocinae the fore flipper is much more square in shape and the digits are more nearly equal. The Phocinae also differ in the position of their nostrils, which are on the anterior end of the snout and more or less vertical. The nostrils of both the Monachinae and the Lobodontinae are nearly on the dorsal surface of the snout and are almost horizontal. As already noted in the various sections on the bones of the skeleton of *Monachus*, these are in general much more like those of the Southern than the

Northern Phocids. The above evidence shows clearly that the Monachinae are more closely related to the Lobodontinae than to the Phocinae.

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PLATE 3

Monachus monachus. Photographs of the specimen from Oran in the Jardin des Plantes, Paris. The animal was blind in its right eye. Phot. J. E. K.

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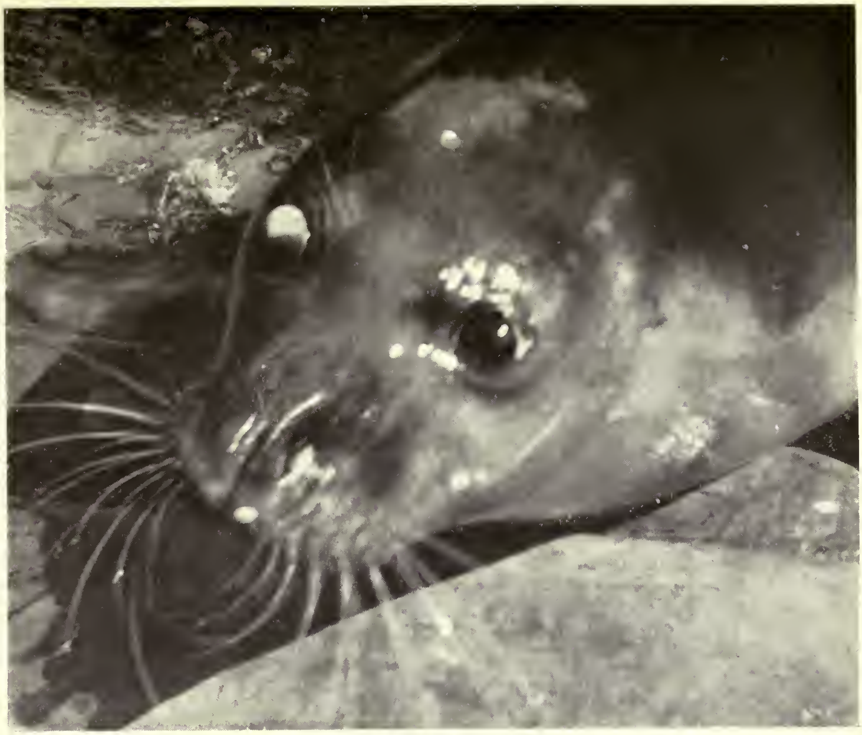
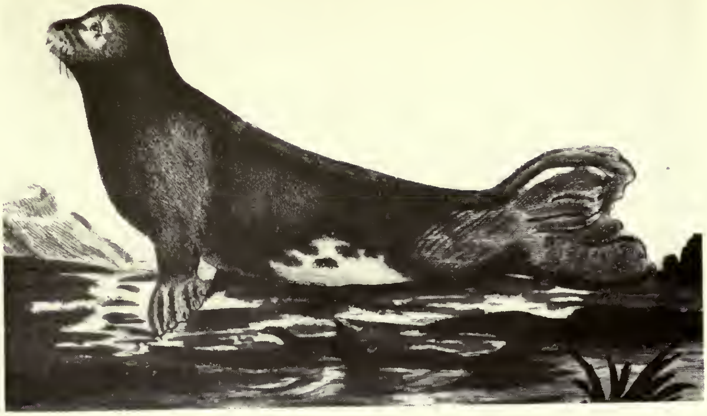


MONACHUS MONACHUS

PLATE 4

Monachus monachus. A. From Hermann, 1779. B. From Buffon, 1782. C. From Pennant, 1793.

PLATE 4



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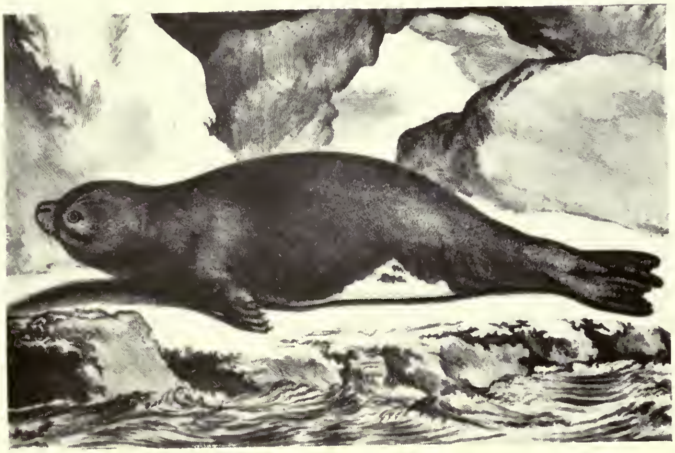

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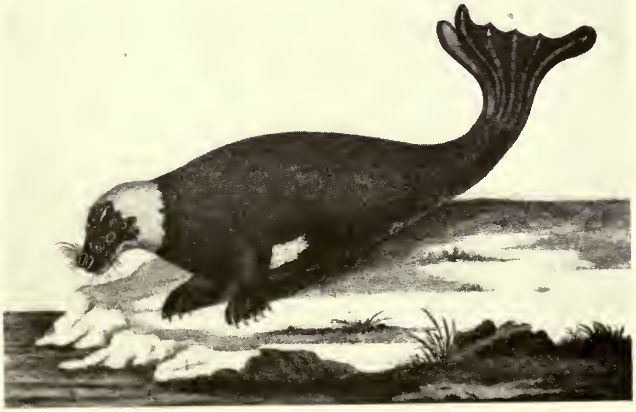

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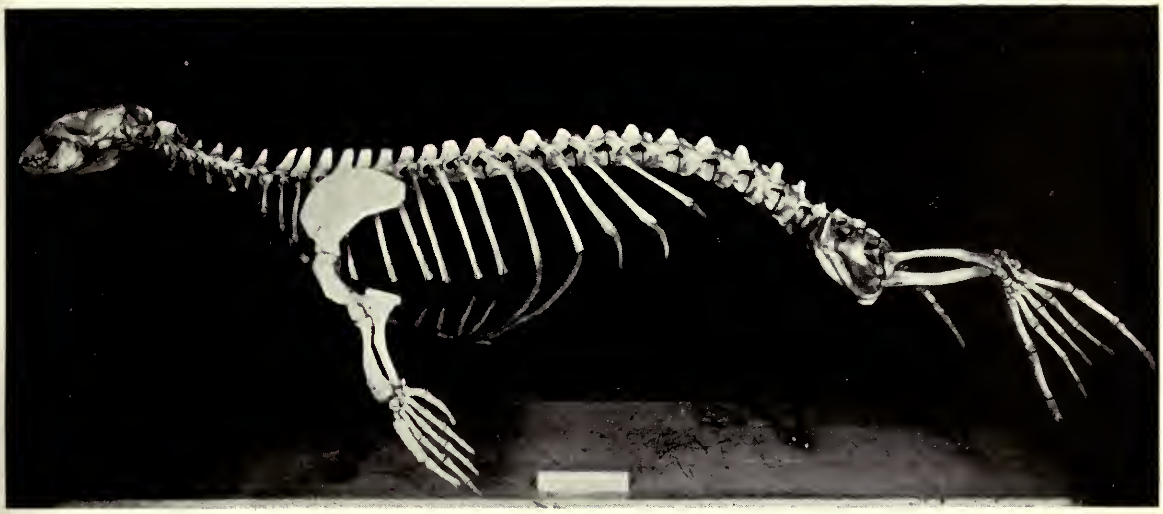
PLATE 5

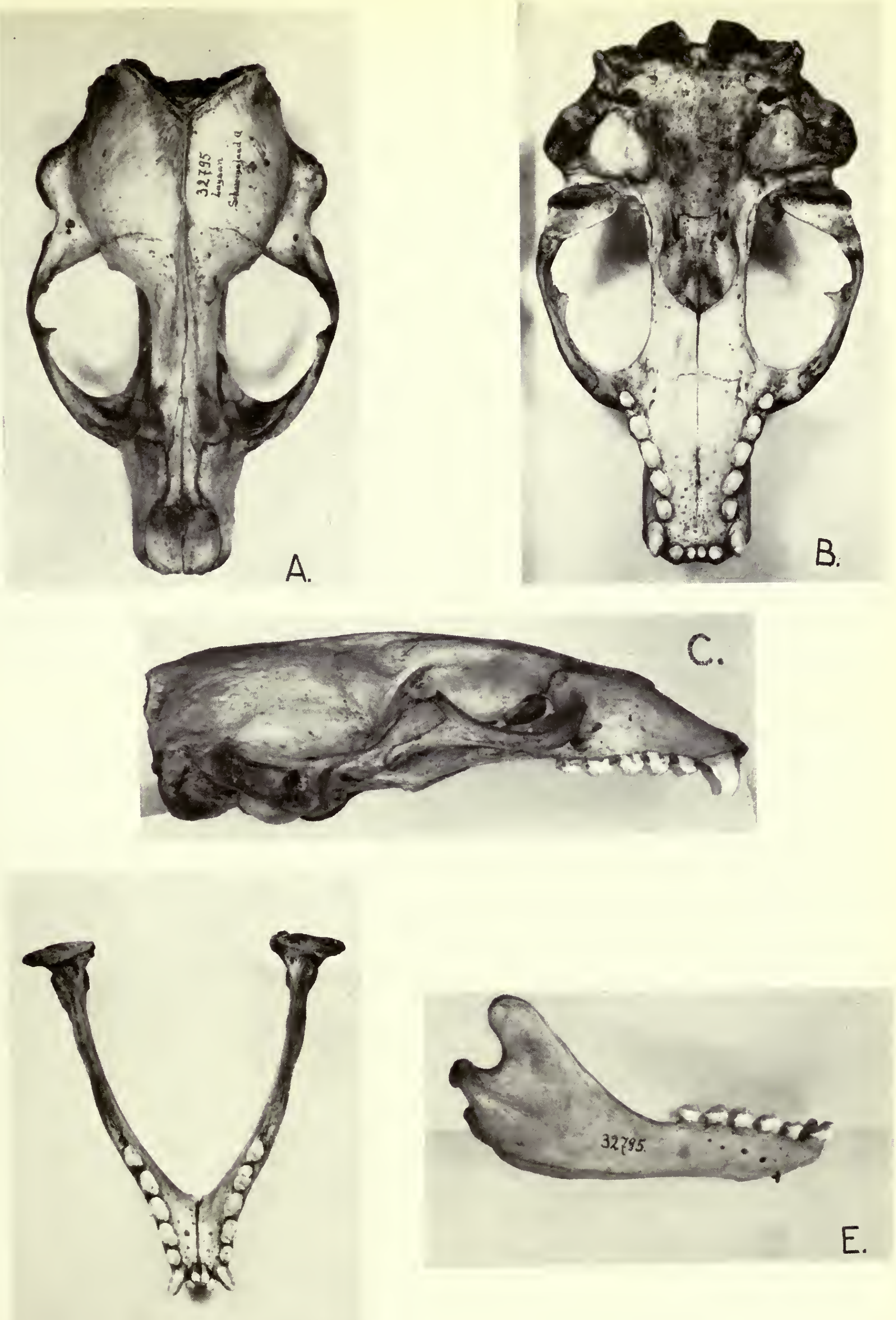
Monachus tropicalis. Lateral view of skeleton 1887.8.5.1.



MONACHUS TROPICALIS

PLATE 6

M. schauinslandi. Skull of type specimen No. 32795, Zoological Museum, Berlin. A. Dorsal view. B. Ventral view. C. Lateral view. D. Dorsal view of lower jaw. E. Lateral view of lower jaw.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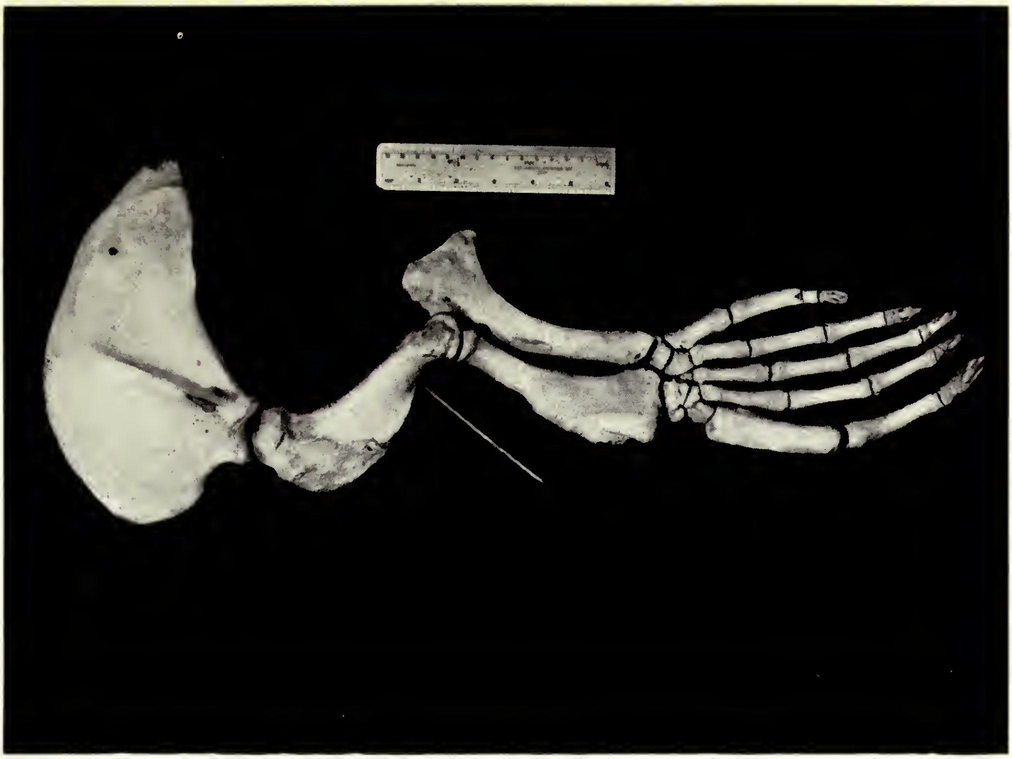
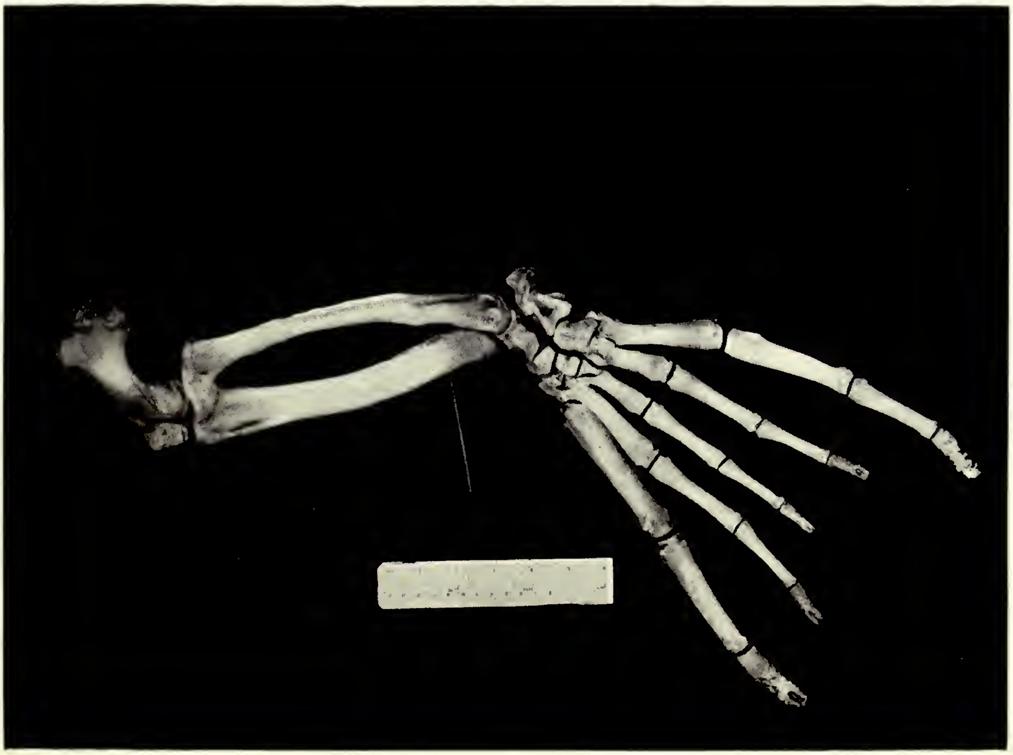
M. SCHAUINSLANDI

PLATE 7

M. tropicalis. A. Fore limb. B. Hind limb.

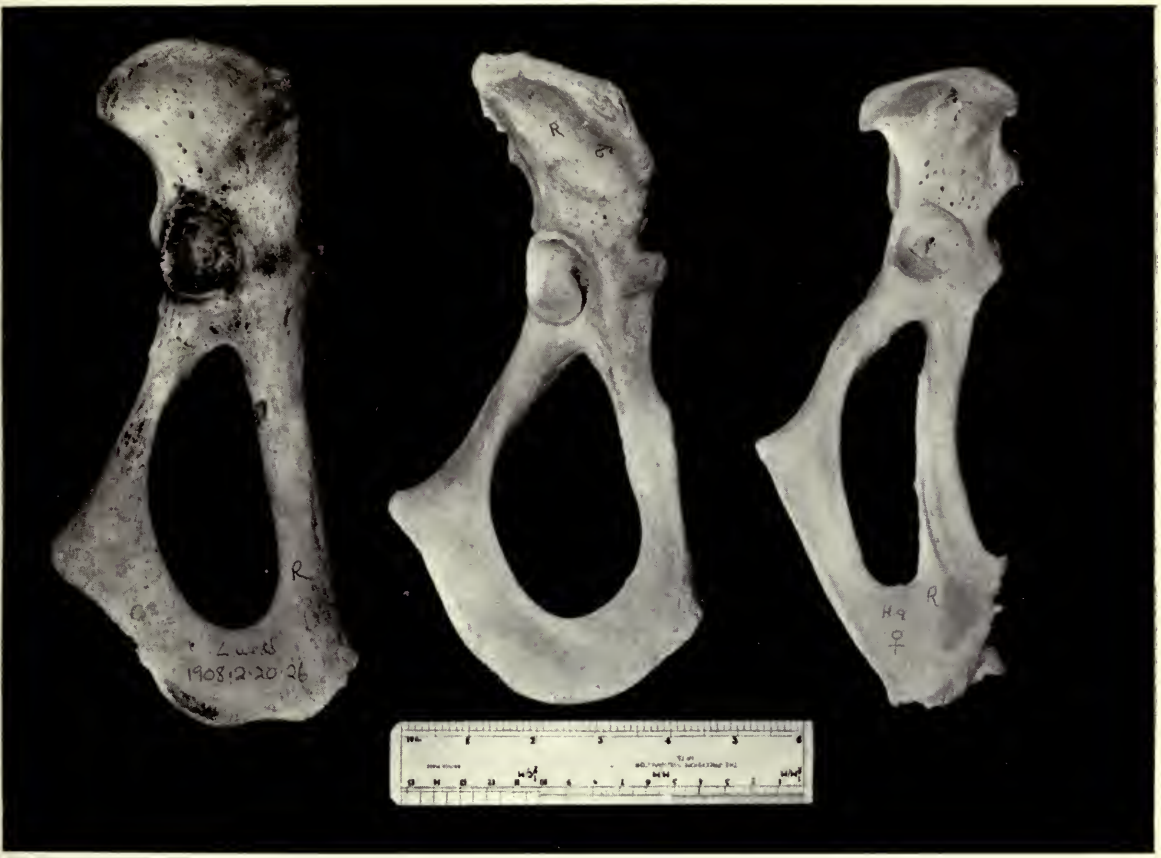




M. TROPICALIS

PLATE 8

Innominate bones of A. *L. weddelli*, B. *M. monachus*, C. *H. grypus*.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THE CEPHALOPODA OF MADEIRA

RECORDS AND DISTRIBUTION

W. J. REES AND G. E. MAUL

NOTES ON THE EUROPEAN SPECIES OF *ELEDONE*

W. J. REES

BULLETIN OF
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ZOOLOGY Vol. 3 No. 6
LONDON: 1956

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Pp. 257—293; *Pls.* 9–10: 4 *Text-Figures*

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THE CEPHALOPODA OF MADEIRA

RECORDS AND DISTRIBUTION

By W. J. REES AND G. E. MAUL

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SYNOPSIS

The cephalopod fauna of Madeira is revised and no fewer than 22 additional species are added to the list, chiefly on account of the examination of the stomach contents of *Alepisaurus ferox* Lowe, *Aphanopus carbo* Lowe and the sperm whale. A total of 18 species (many of them rare and seldom taken in the nets of deep sea expeditions) are recorded from *Alepisaurus ferox*. The following little known species have been found in the stomachs of sperm whales at Madeira: *Tetronychoteuthis dussumieri* (Orbigny), *Lepidoteuthis grimaldi* Joubin and *Architeuthis* sp. The composite fauna is analysed and compared with that of the Mediterranean.

I. INTRODUCTION

This preliminary paper on the cephalopod fauna of Madeira has its origins in an investigation of the stomach contents of the voracious fish, *Alepisaurus ferox* Lowe. The work at Madeira was pursued for some years prior to the despatch of all the cephalopoda taken (together with representative local collections) to the British Museum (Natural History) for identification. The material yielded many species scarce in collections and it was deemed an opportune time to produce a new list of Madeiran cephalopods.

This list is rich in the names of seldom-recorded species, chiefly because the fishes *Alepisaurus ferox, Aphanopus carbo* Lowe and the sperm whale have been examined for stomach contents. The occurrence of the various rare species are noted in the main part of the text, but special attention is drawn to the records of *Lepidoteuthis grimaldi* Joubin, *Tetronychoteuthis dussumieri* (Orbigny), *Histioteuthis bonelliana* (Férussac) and *Architeuthis* from the sperm whale.

In this preliminary paper we have not given full descriptive accounts of the species found ; this is reserved for further accounts of interesting species either jointly or independently.

II. A SUMMARY OF PREVIOUS RECORDS

The first record of a cephalopod to be recorded in scientific literature from the vicinity of Madeira was of a Taonid which d'Orbigny referred to *Loligopsis pavo* Lesueur in the great *Histoire des céphalopodes acetabulifères* (1835–1848). It was later pointed out by Rochebrune (1884) and Hoyle (1884) that d'Orbigny had confused two species under this name and the Madeiran specimen (taken in sight of Madeira by the naturalist Dussumier) was redescribed by the former under the name *Phasmatopsis cymoctypus*.

Robert MacAndrew, who dredged extensively on the coast of Spain and Portugal, both in the Atlantic and in the Mediterranean, does not mention a single cephalopod from his dredgings at Madeira (1849–50).

White and Johnson, in their *Handbook of Madeira* (1860) list the following six species :

Loligo vulgaris Lamarck.
Sepia officinalis L.
Octopus vulgaris Lamarck.
Octopus cuvieri (= *O. macropus* Risso).
Argonauta argo L.
Ocythoë tuberculata Rafinesque.

In their second edition (1885) the fourth and last species are not listed. Hoyle (1885, p. 69) confirmed the occurrence of *Argonauta argo* at Madeira in his Challenger Report.

More species were added to the list by Girard (1892) who reported on the collections of the Abbé Ernest Schmitz of the Seminário do Funchal, adding or confirming the existence of the following at Madeira :

Loligo forbesi Steenstrup.
Spirula peronii Lamarck[1] (=*Spirula spirula* L.).
Sepia filliouxii Lafont (= *S. officinalis*).
Todarodes sagittatus (Lamarck).
Ocythöe tuberculata Rafinesque.
Octopus tuberculatus Blainville.[2]

Girard was aware of the differences between *L. vulgaris* and *L. forbesi* and as the species submitted to him by Schmitz proved to be *L. forbesi*, the former species was dropped from the list ; nor was he able to confirm the existence of *O. macropus* in the area.

---

[1] Apparently empty shells.

[2] Presumed here to be a juvenile specimen of *O. vulgaris*.

Watson (1897) added no new species to the list of Madeiran cephalopods but confirms that *O. vulgaris* is a common species and states that *Sepia officinalis* is rare.

From 1890 onwards the various deep sea expeditions have taken cephalopods in the N. Atlantic, sometimes near, sometimes some distance off Madeira, and the list compiled by Nobre (1937) includes 20 species of which several have been taken a considerable distance away and could not be termed local fauna. Some of the species which he records were taken as far west from Madeira as the African coast is to the east of it. The following species were taken too far away to be retained as local Madeiran records :

Sepietta oweniana (Orbigny).
Onychia caribaea Lesueur.
Brachioteuthis riisei (Steenstrup).
Histioteuthis bonelliana (Férussac).
Taonius pavo (Lesueur).
Japetella diaphana Hoyle.

As Girard's *Octopus tuberculatus* probably falls into the synonymy of *O. vulgaris*, Nobre's list becomes amended to 13 cephalopods known from the immediate vicinity of Madeira. To these may be added Joubin's record of *Leachia cyclura* (1920).

III. ADDITIONS TO THE FAUNA

The Madeiran archipelago has a much richer cephalopod fauna as our investigations have shown, and we do not think we have by any means exhausted the numbers of species which should occur off Madeira. A great many other cephalopods known from the central North Atlantic remain to be reported from this area. Below is given a list of 22 additional species which we are now recording from Madeira.

Heteroteuthis dispar (Rüppell).
Loligo vulgaris Lamarck.
Abraliopsis morisii (Verany).
Enoploteuthis leptura (Leach).
Pyroteuthis margaritifera (Rüppell).
Cucioteuthis unguiculata (Molina).
Tetronychoteuthis dussumieri (Orbigny).[1]
Lepidoteuthis grimaldi Joubin.[1]
Onychoteuthis banksi (Leach).
Architeuthis sp.
Histioteuthis bonelliana (Férussac).
Ommastrephes pteropus Steenstrup.
Thysanoteuthis rhombus Troschel.
Chiroteuthis veranyi (Férussac).
Mastigoteuthis schmidti Degner.

---

[1] These two species are here recorded from the stomachs of sperm whales taken at Madeira. It is hoped to provide a full description in another paper.

Taonius pavo (Lesueur).
Cranchia scabra Leach.
Japetella diaphana Hoyle.
Eledonella pygmaea Verrill.
Vitreledonella richardi Joubin.
Alloposus mollis Verrill.
Tremoctopus violaceus delle Chiaje.

Family Spirulidae

Spirula spirula L.

Spirula peronii, Girard, 1892, p. 219; Watson, 1897, p. 318, Nobre, 1937, p. 5.

This species is known only from the dead shells at Madeira; these are cast up on the beaches of Porto Santo occasionally and are also known from Caniçal (Girard). Bruun (1943) reporting on the living *Spirula* captured by the " Dana " expeditions, believed that this species inhabits the continental slope, living at depths not exceeding 1750 metres.

Family Sepiidae

Sepia officinalis L.

Sepia officinalis, White & Johnson, 1860; Johnson, 1885; Watson, 1897, p. 316; Nobre, 1937, p. 5.
Sepia fillouxii, Girard, 1892, p. 219.

Material seen :

1 specimen, dorsal mantle length of 205 mm. (Maul collection No. 144).

According to Watson (1897), *Sepia officinalis* is rare at Madeira, but the species is very common all the year round at Madeira and adult specimens measuring about 25 cm. (in dorsal mantle length) are often seen at the local fish market. The species goes by the name of *Chouco* and is eaten by the local population.

Family Sepiolidae

Heteroteuthis dispar (Rüppell)

Material seen : All except No. 3281 from the stomachs of *Alepisaurus ferox*.

No. 3281, 1 mutilated specimen, dorsal mantle length 20 mm. from the stomach of *Aphanopus carbo*, 10.i.51.
No. 3365, 1 specimen, dorsal mantle length 25 mm., 10.iv.1952.
No. 3490, 4 specimens, dorsal mantle lengths of 25, 28, 29 and 20 mm.—no date.
No. 3802, 1 specimen, dorsal mantle length of 22 mm.—no date.
No. 3848, 2 specimens, dorsal mantle lengths of 8 and 12 mm.—no date.

This sepiolid has not previously been taken at Madeira, and although reported from numerous stations in the Mediterranean (Degner, 1925). it has been found on comparatively few occasions in the Atlantic. Each major expedition has, however, secured specimens; those found nearest to Madeira being those captured by the "Talisman" (29° 2′ N., 14° 49′ N.) between the Canaries and the African coast (Fischer & Joubin, 1907), and those of the "Thor" from just outside the Straits of Gibraltar (Degner, 1925). *Heteroteuthis dispar* is often regarded as a deep sea cephalopod, but it is difficult to justify this claim, which seems to be based on the fact that the species has a luminous secretion. To quote Harvey (1952, p. 283): "It is sometimes said that the luminous secretion of deep sea *Heteroteuthis* has replaced the ink of surface dwellers. This black fluid forms a poisonous smoke screen which confounds the enemy while the squid makes a getaway. Although it is not true that the luminous secretion has completely replaced the ink, it may serve a similar purpose—to draw the attention of the enemy to a mass of lighting material, while the squid moves off in another direction." However, an examination of Degner's details of capture in the Mediterranean and Atlantic shows that captures were more frequent with only 300 metres of wire out than in deeper hauls, and it can be reasonably assumed that the net was fishing at only half or less than half this depth. The fact that *Heteroteuthis* has retained its ink sac is also an indication that it can and does live above the threshold of light. Whether it can also live below the threshold of light is so far unknown. As an item in the food of *Alepisaurus ferox*, it probably occurs at the depths at which this fish is taken on tunny hooks at Madeira. It is also a regular item in the diet of the long-finned albacore (*Germo alalunga*) in the Bay of Biscay (Bouxin & Legendre, 1936, p. 36), and it has been reported from the stomach of the dolphin (*Delphinus delphis*) by Joubin (1900, p. 10).

Sepietta oweniana (Orbigny)

Sepiola scandica, Fischer & Joubin, 1906, p. 204.
Sepietta oweniana, Bouxin & Legendre, 1936, p. 32; Nobre, 1937, p. 5.

Material seen:

No. 2812, 2 specimens, dorsal mantle lengths of 12 and 17 mm., Funchal Harbour, 12.iii.1943.

The "Travailleur" took this species in position 32° 40′ N., 18° 54′ W., some distance to the south-west of Madeira. Its occurrence at Madeira is confirmed from two specimens we have seen.

Family LOLIGINIDAE

Loligo vulgaris Lamarck

Material seen:

No. 2966, 1 juvenile, no data.
No. 3164, 5 juveniles from Funchal Harbour, 4.v.1950.
No. 3848, 1 juvenile, dorsal mantle length of 7 mm. from stomach of *Alepisaurus ferox*.

The specimens from Funchal Harbour are juveniles of only 30–35 mm. in dorsal mantle length. *Loligo vulgaris* is recorded as far north as the coast of Denmark, but it is doubtful whether it breeds anywhere north of the latitude of Ushant at the mouth of the English Channel. As a Lusitanian species it is well known in the Mediterranean and on the Mauritanian coast, while recently Adam (1952) has demonstrated that it occurs off the Congo and as far south as Algoa Bay. It has been reported from the Canary Islands (Odhner, 1931) and, although said to occur at the Azores (Drouet, 1858), its presence there requires confirmation.

Loligo forbesi Steenstrup

Loligo forbesii, Girard, 1892, p. 219 ; Nobre, 1937, p. 6.

No. 4355, Funchal Market 1 ♂ of 270 mm. in dorsal mantle length.

Girard based his identification of this species on many examples sent to him by the Abbé Ernest Schmitz of Funchal. This species has often been reported from the neighbouring African coast. Locally, *Loligo* goes by the name of *Lula da costa*, but it is not known whether the two species are confused under this name. It is very common in winter, and as an article of food stands next to *O. pteropus* in importance. Market specimens range from about 200 mm. to 500 mm. in dorsal mantle length.

Abralia veranyi (Rüppell)

Abralia veranyi, Berry, 1926, p. 257.
Abralia veranyi, Nobre, 1937, p. 7.

Material seen :

No. 2664, 1 specimen of 47 mm. dorsal mantle length, Funchal Harbour, at night, 16.x.1941.
No. 2964, no data—5 specimens, 37–50 mm. in dorsal mantle length.
No. 3514, Funchal Museum (no date).

This luminous squid is a Mediterranean-Atlantic species ; most of the records of its occurrence are from the Mediterranean (Messina, Nice, Genoa, Naples and Toulon), while in the Atlantic (apart from Madeira) it has been found at comparatively few places, viz : Cockburn Town, San Salvador Island (Adam, 1941) and off the Congo (Adam, 1952).

These specimens provide additional records for Madeira. No. 3514, a male, has the left ventral arm hectocotylized just as figured by Adam (1952, p. 63, fig. 25E). This specimen has a dorsal mantle length of 42 mm. One of the female specimens (Lot No. 2964) has a dorsal mantle length of 50 mm. ; this is considerably bigger than Adam's largest specimens, which were up to about 40 mm. in dorsal length (Adam, 1952, p. 70).

Abraliopsis morisii (Verany)

Material seen :

No. 3848, 6 specimens of 8–25 mm. in dorsal mantle length from the stomach of *Alepisaurus ferox*.

This is the first time this small luminous squid has been recorded from Madeira and from the stomach of *Alepisaurus ferox*. Records of this species from the Mediterranean and the Atlantic are fairly numerous (see Chun, 1910).

Enoploteuthis leptura (Leach)

Material seen :

No. 2664, Funchal Harbour at night, 16.x.1941, 1 specimen.
No. 2963, Madeira, 1 specimen, no data.
No. 3487, Funchal Harbour at night, 1.vi.1946, 1 specimen.

These are the first Madeiran records of this rather scarce cephalopod. It is known from the African coast and Pacific (Férussac & d'Orbigny, 1835–1848) and a juvenile from the Atlantic (position 0° 29′ N., 18° 57′ W.) was captured by the Deutsche Südpolar-Expedition and figured by Chun (1910, Taf. xl, figs. 5 and 6) in the " Valdivia " report.

Pyroteuthis margaritifera (Rüppell)

Material seen :

No. 2961, 2 specimens, dorsal mantle length of 35 mm., from stomach of *Alepisaurus ferox*, March and April, 1944.

This is another well known Mediterranean-Atlantic, luminous cephalopod. Joubin (1924, p. 52) reported it from the Azores but it does not seem to have been recorded from Madeira, neither has it been recorded as an item in the diet of *Alepisaurus ferox*. The " Thor " took specimens in the Eastern Mediterranean with 200–300 metres of wire out, so that the species can be assumed to exist up to 100 metres of the surface.

Family OCTOPODOTEUTHIDAE

Cucioteuthis unguiculata (Molina)

Cucioteuthis unguiculata, Joubin, 1900, p. 51 ; Nobre, 1937, p. 6.

The " Princess Alice " took this species in position 32° 32′ 10″ N., 19° 24′ 40″ W., to the west of Madeira. There is a large brachial crown, in the Municipal Museum, Funchal, from a specimen which was found dead floating at the surface near the shore to the west of Funchal.

Onychia caribaea Lesueur

Teleoteuthis jattai Joubin, 1900, p. 67.
Teleoteuthis caribaea, Nobre, 1937, p. 7.

Nobre includes this species in his list of Madeiran cephalopods, but the position at which this species was taken by the " Princess Alice " (1897) Cruise, St. 812, 31° 04′ N., 27° 11′ W.) is nearly as far to the south-west of Madeira as these islands are from the African coast. The species must therefore be omitted from the list.

Onychoteuthis banski (Leach)

Material seen :

No. 2455, no data, 1 specimen of 100 mm. in dorsal mantle length.
No. 3507, no data, 1 specimen of 130 mm. in dorsal mantle length.
No. 2965, no data, 1 poorly preserved specimen of 35 mm. dorsal mantle length.
No. 3571, 1 specimen of 48 mm. dorsal mantle length, from stomach of *Alepisaurus ferox*, 4.xii.1952.
No. 3848, 45 specimens, dorsal mantle lengths of 10, 13, 21–24 mm., stomach of *Alepisaurus ferox*.
No. 3509, 1 mutilated juvenile, dorsal mantle length 24 mm., from the stomach of *Alepisaurus ferox*.

Onychoteuthis banksi is here recorded for the first time from Madeira. No. 2965 is in poor condition and only provisionally referred to this species.

This is a well-known oceanic surface species which, in the neighbourhood of Madeira, was taken in position 30° 54′ N., 24° 11′ N., by the Prince of Monaco in his 1912 cruise (Joubin, 1924, p. 48). Other nearby records for the " Terra Nova " and the " Ara " are given by Rees (1949, p. 43) who drew attention to the habit of " flying " in this species. New records of specimens being found on the deck of ships are given by Adam (1952, p. 77).

Family ARCHITEUTHIDAE

Architeuthis sp.

A sperm whale, harpooned off São Lourenço on 12th June, 1952, vomited a squid which had evidently just been swallowed because the latter still exhibited some signs of life. This squid was large, with a weight of 150 kilograms, and could only have been a species of *Architeuthis*. The following measurements were taken :

Overall length (i.e. including tentacles) . .	10,600 mm.
Dorsal mantle length	1,860 ,,
Length of tentacles	8,500 ,,
Length of arm	2,800 ,,
Circumference of mantle	1,360 ,,
Circumference of tentacles	330 ,,

Architeuthis was taken by the French steamer " Alécton " between Madeira and Teneriffe in November, 1860, and the species was subsequently given the name *Loligo bouyeri* by Crosse and Fischer (1862, p. 138). A number of species of *Architeuthis* have been described since Verrill's classical monograph and it is by no means certain how many kinds there are. Fragments of the above specimen are kept in the Museu Municipal, Funchal, and it is hoped to present a more detailed description in another paper.

Family HISTIOTEUTHIDAE

Histioteuthis bonelliana (Férussac)

Histioteuthis rüppelli, Joubin, 1900, p. 98.
Histioteuthis bonelliana, Nobre, 1937, p. 6.

Material seen :

No. 3905, 1 specimen, dorsal mantle length of 53 mm., from stomach of *Aphanopus carbo*, 30.x.1953.

Nobre records this species as Madeiran on the basis of an arm found in position 41° 0′ N., 12° 15′ W., by the " Princess Alice " in 1894 (Joubin) ; this position is off the north coast of Portugal, so that this could not be justified as a Madeiran record of this species. *Histioteuthis* does occur, however, around Madeira, as recorded above, and we are indebted to Mr. H. M. Sieyes for a photograph of a large brachial crown of this species found in the stomach of a sperm whale captured off São Laurenço lighthouse, Madeira on 12th June, 1952. It is interesting to note that this sperm whale feeds on this species at Madeira, as at the Azores and elsewhere. The specimen from the stomach of *Aphanopus carbo* was much smaller, with an overall length length of about 170 mm. It is noteworthy that Verrill (1880, p. 234) recorded *H. bonelliana* from *Alepisaurus ferox* (as *H. collinsii*).

Family BRACHIOTEUTHIDAE

Brachioteuthis riisei (Steenstrup)

Tracheloteuthis riisei, Joubin, 1924, p. 75.
Brachioteuthis (*Tracheloteuthis*) *riisei*, Nobre, 1937, p. 6.

This wide-ranging surface cephalopod is included in the Madeiran fauna by Nobre on the strength of a record of capture of this species in position 31° 45′ N., 20° 17′ W., by the " Princess Alice " (Joubin). This is some distance south and west of Madeira, but such a widely distributed species is almost certain to be found in this area.

Family OMMASTREPHIDAE

Todarodes sagittatus (Lamarck)

Todarodes sagittatus, Girard, 1892, p. 220.
Ommastrephes sagittatus, Nobre, 1937, p. 8.

Material seen :

No. 3355, 1 juvenile, dorsal mantle length of 83 mm. from the stomach of *Alepisaurus ferox*, 8.iv.1952.

No. 3356, 1 juvenile, dorsal mantle length 86 mm. from the stomach of *Alepisaurus ferox*, 8.iv.1952.

No. 3363, 1 juvenile, dorsal mantle length 85 mm. from the stomach of *Alepisaurus ferox*.

No. 4347, Funchal Market, 1 specimen of 185 mm. in dorsal mantle length.

Madeiran records in the literature are few and are based on the following specimens: 1 ♀ taken by Schmitz, 1 ♀ by Nunes. To these may be added the specimens from the stomach of *Alepisaurus ferox* noted above.

The sucker rings of the tentacles are mostly absent: the very long-sucker-bearing region of the tentacle, extending for the greater part of its length, the almost smooth, large tentacular rings and the presence of four rows of suckers near the tip of the tentacles indicate that the species is *T. sagittatus*. Locally *Todarodes* is called *Cartucho*; it is extremely common on the fishing grounds in March, April and May. It is also taken during other months, but it is rare at these times.

As a common cephalopod on the fishing grounds of the eastern North Atlantic and the Mediterranean, *Todarodes* is preyed on by a number of animals, including the dolphin, *Delphinus delphis* (Joubin, 1895, p. 32), *Germo alalunga* (Bouxin and Legendre, 1936) and *Gadus calliarias* (*Michael Sars* Stations 7, 86, 352 and 115). Joubin (1895, 1900, 1920 and 1924) also reported various ommastrephid fragments, some of which probably belong to this species, from *Polyprion americanum* and *Grampus griseus*.

Ommastrephes pteropus Steenstrup

Material seen:

Nos. 65 and 66, 2 fragments, Funchal Harbour, 16.iv.1941.
No. 193, 1 juvenile, dorsal mantle length 58 mm., 10.v.1940.
No. 3443, 1 specimen, dorsal mantle length 270 mm.—no data.
No. 3678, 1 juvenile, dorsal mantle length 50 mm. from stomach of *Alepisaurus ferox*, 25.iii.1953.
D. W. Tucker Collection, No. 605, 1 juvenile, dorsal mantle length 80 mm.
D. W. Tucker Collection, Nos. 639–644, 6 half-grown specimens, gaffed at night on Madeiran fishing grounds, August, 1953.

All these specimens have been referred to *O. pteropus*; some of them might equally well have been referred to *O. bartrami* as we find that the diagnostic key given by Pfeffer (1912, p. 465) is unreliable and our specimens clearly belong to one species.

Adam (1952, p. 110) also noted the unreliable nature of the connective apparatus on the tentacles as a means of separating *bartrami* from *pteropus*. The number of suckers, proximal to the nearest connective button, will vary as new buttons develop with the growth of the tentacle, as indicated in one of our larger specimens where there is a rudimentary button; this points to the great need for a revision of these species with more material than we have at our disposal.

The relationships of these two species to *Ommastrephes caroli* is equally puzzling. In the species *caroli* the lateral membrane is a broad triangular flap in adult specimens (Rees, 1950, pl. 1) while in younger specimens it is much narrower (see Hertling, 1938). Our specimens from Madeira (those of 2–3 ft. in total length) possess narrow lateral membranes on the third arms which might conceivably develop into the characteristic paper-thin flaps of *caroli*. As in the latter their chromatophores are closely set and a deep chestnut-brown in colour.

Ommastrephes pteropus is very abundant during the summer months of July, August and September and is extensively used for baiting the tackle for *Aphanopus carbo*, tunny and other fish. It is found in great numbers in locally caught *Germo obesus*. Large quantities of this squid, which goes under the local name of *Pota de limão* or *Lula de limão*, are sold in the fish market for consumption by the local people, who greatly appreciate it as food. The large, lemon-coloured dorsal mark has been observed to flare up with a bright light when the animal is gaffed.

Ommastrephids :

No. 2957, 1 juvenile, dorsal mantle length of 50 mm. from stomach of *Alepisaurus ferox*, March–April, 1944.

No. 3848, 3 juveniles, dorsal mantle length of 17, 20 and 25 mm. from the stomach of *Alepisaurus ferox*.

No. 193, 1 juvenile, dorsal mantle length of 65 mm. from the stomach of *Alepisaurus ferox*, 10.v.1940.

These fragmentary specimens are in poor condition and we have not been able to identify them.

Thysanoteuthis rhombus Troschel

Material seen :

1 specimen, dorsal mantle length of 350 mm., taken at Funchal.

This is the first record of this powerful surface species from Madeira. Some years ago a school of about 20 came close inshore, and this is the only specimen it was possible to save for examination. Little is known about its distribution, but it occurs in the Mediterranean (Naef, 1923–1928) and has been reported from the Cape of Good Hope by Barnard (1934). It is likely, however, to be a cosmopolitan warm-water species, as Sasaki (1929) has recorded it from a number of localities in Japanese waters.

Chiroteuthis veranyi (Férussac)

Material seen :

No. 3685, 1 *Doratopsis* larva of 80 mm. in overall length. Coll. A. A. Nunes, 8.vii.1948.

This larva was taken at the Pontinha at the surface at night in the light of an electric lamp suspended over the water.

It is a well-known Mediterranean-Atlantic species whose larva is frequently taken at places like Messina and Villefranche, where there is upwelling from deep water. The closely related species *Doratopsis exophthalmica* was taken by the " Valdivia" in position 31° 59′ N., 15° 5′ W. to the south-east of Madeira.

Published records of *C. veranyi* from the North Atlantic are few (see Adam, 1952, p. 111), but to judge from the number of specimens recovered from the stomachs of germon fished in the Bay of Biscay the species is not as rare as the absence of records suggests (Bouxin and Legendre, 1936).

Mastigoteuthis schmidti Degner

Material seen :

1 specimen, dorsal mantle length of 107 mm., from the stomach of *Alepisaurus ferox*, December, 1944.

There are no previous records of *Mastigoteuthis* from Madeira and this specimen is only provisionally referred to *M. schmidti* because we recognize the need for a complete revision of the large number of species described from the Atlantic. As regards the proportions of mantle and fin the species is very similar to *M. schmidti*.

Family CRANCHIIDAE

Leachia cyclura Lesueur

Leachia cyclura, Joubin, 1920, p. 68.

Material seen :

No. 3513, 1 specimen, overall length 145 mm. from stomach of *Alepisaurus ferox*—no date.

No. 3848, 1 juvenile, dorsal mantle length of 23 mm. from stomach of *Alepisaurus ferox*.

Leachia cyclura was taken by the Prince of Monaco on the fishing grounds of Madeira in 1901 (Stn. 1235, 8th September, 32° 34′ N., 17° 45′ W.). This species has rarely been captured in the Atlantic, and since it was described from the Atlantic coast of N. America by Lesueur (1821), it has been recorded by Joubin only from Madeira, the Azores and the Sargasso Sea. It is known from other oceans also.

Cranchia scabra Leach

No. 3497*a*, 1 specimen, overall length of 110 mm. from stomach of *Alepisaurus ferox*.

No. 3497*b*, 1 specimen, Funchal Harbour, at night.

No. 3497*c*, 1 specimen, overall length 105 mm. from stomach of *Alepisaurus ferox*.

This species is well known from the sub-tropical and tropical areas of the Atlantic and other oceans, but does not appear to have been reported from Madeira. It is also recorded for the first time from the stomach of *Alepisaurus ferox*.

There is no particular reason for supposing that this species is a deep-water animal. Its presence in the upper 200 metres has been proved by the Deutsche Südpolar Expedition, which took specimens at 20 and 40 metres depth. It should be noted that records from 2,000 and 3,500 metres by the " Valdivia " were made with open nets (Chun, 1910).

Taonius pavo (Lesueur)

Taonius pavo, Joubin, 1900, p. 106; Nobre, 1937, p. 8.

Material seen:

No. 3902, 1 specimen without tentacles, partly macerated, from the stomach of *Alepisaurus ferox*, 26.xi.1953.

This specimen agrees favourably with the specimen figured by Joubin (1900, p. 106, pl. viii and ix), but the colour is of a deep reddish purple. Our specimen has a dorsal mantle length of 275 mm. and a total length of 385 mm.

This example, from the stomach of *A. ferox*, is the first to be found at Madeira. The specimen taken by the Prince of Monaco in 1897 (Stn. 817, position 30° 42′ N., 27° 32′ W. was found well out in the Atlantic and a considerable distance from Madeira.

Taonius pavo has all the appearance of being a bathypelagic species, and we have wondered whether the occurrence of this squid (and also some others, notably, *Mastigoteuthis schmidti* and *Eledonella pygmaea*) in this fish can be explained by local upwelling of deep water bringing these species near the surface.

Taonius cymoctypus (Rochebrune)

Loligopsis pavo, Orbigny, 1835–1849, p. 321 (*pars*).
Phasmatopsis cymoctypus Rochebrune, 1884, p. 15, pl. 1.
Taonius pavo, Girard, 1892, p. 220; Nobre, 1937, p. 8.

The only specimen known of this cephalopod was taken within sight of Madeira by the French naturalist Dussumier and was confused with *T. pavo* by d'Orbigny. Later Rochebrune demonstrated that it was a distinct species. A new description of this curious squid is greatly needed.

Order OCTOPODA

Family BOLITAENIDAE

Japetella diaphana Hoyle

Japetella diaphana, Thore, 1949, p. 23, fig. 14.
Bolitaenella diaphana, Nobre, 1937, p. 3.

Material seen:

No. 2958, 4 specimens, total length *ca.* 50 mm., stomach of *Alepisaurus ferox*, March–April, 1944.

No. 3357, 1 specimen, total length *ca.* 50 mm., from stomach of *Alepisaurus ferox*, 8.iv.1952.

No. 3495, 2 specimens, total length of 50 and 70 mm., stomach of *Alepisaurus ferox*.

No. 3496, 1 specimen, total length 70 mm., ? stomach of *Alepisaurus ferox*.

No. 3569, 2 specimens, total lengths 55 and 80 mm., stomach of *Alepisaurus ferox*, 4.xii.1952.

No. 3594, 1 specimen, total length 65–70 mm., stomach of *Alepisaurus ferox*, 1.iii.1953.

No. 3903, 1 damaged specimen, total length 85 mm., stomach of *Alepisaurus ferox*, 26.x.1953.

There are numerous records of this pelagic octopod in the North Atlantic, in the triangle, Canaries, Gibraltar, Azores (Thore, 1949, fig. 14, p. 23), but the first positive records from Madeiran fishing grounds are given above.

Bouxin & Legendre (1936, p. 12) reported finding this species (one specimen in each of three stomachs) in the germon (*Germo alalunga*) captured in the Bay of Biscay. It is now recorded for the first time from *Alepisaurus ferox* and appears to be a regular item in the diet of this fish.

For the *Bolitaenella diaphana* of Nobre, see *Eledonella pygmaea*.

Eledonella pygmaea Verrill

Eledonella diaphana, Joubin, 1900, p. 37, pl. 2, figs. 5–7.

Material seen :

No. 3800, 1 ♀ total length 150 mm., from the stomach of *Alepisaurus ferox*, no date.

Eledonella pygmaea is less common than the preceding species. It has not previously been recorded from Madeira or from the stomach of *Alepisaurus ferox*.

The " Princess Alice " (Joubin, 1900) took this species between Madeira and the African coast and there are more recent records of specimens taken by the " Dana " to the west and north of the Madeiran archipelago (Thore, 1949, fig. 41, p. 49).

Family VITRELEDONELLIDAE

Vitreledonella richardi Joubin

Vitreledonella alberti Joubin, 1924, p. 38 ; Nobre, 1937, p. 3.

This species had been included in a list of Madeiran cephalopods by Nobre (1937), who quotes Joubin's record of a specimen taken to the N.W. of Madeira (position, 33° 40′ N. to 33° 52′ N., 19° W. to 19° 16′ W.) by the Prince of Monaco.

Family OCTOPODIDAE

Octopus vulgaris Lamarck

Octopus vulgaris, White and Johnson, 1860 ; Johnson, 1885 ; Girard, 1892, p. 218 ; Watson, 1897, p. 296 ; Nobre, 1937, p. 3.

Octopus tuberculatus, Girard, 1892, p. 218 ; Nobre, 1937, p. 4.

Octopus rugosus, Robson, 1929.

Material seen :

British Museum :

B.M. No. 1898.5.10.2, Porto Santo, Madeira, Coll. H. S. Wellcombe (Robson, 1929, as *O. rugosus*).

B.M. No. 1912.12.31.118–119, Porto Santo, Madeira, 60 fms., R. Kirkpatrick (Robson, 1929, as *O. rugosus*).

Funchal Market from mouth of *Conger conger*, 18.viii.1953, Coll. D. W. Tucker.

Funchal from a tide pool, 28.viii.1953, Coll. D. W. Tucker.

Funchal Museum :

No. 2460, 1 post-larva.

No. 140, 1 specimen, dorsal mantle length 90 mm.

No. 3287, from the stomach of *Aphanopus carbo*.*

The common octopus, which goes by the local name of *polvo*, is very common all the year round at Madeira and is on sale in the fish market. The fact that it is eaten by the local population may account for the scarcity of specimens available for examination. It is found, too, at the Cape Verde Islands, the Canaries and the Azores. Juvenile octopods mentioned under the name *Octopus tuberculatus* seem to belong to *O. vulgaris*.

Octopus macropus Risso

Octopus cuvieri, Girard, 1892, p. 219 ; White & Johnson, 1860 ; Nobre, 1937, p. 4.

Material seen :

Funchal Museum,—

No. 39, 1 ♀, total length 475 mm., Câmara de Lobos, 30.xi.1940.

No. 139, 1 ♂, total length 1,010 mm.—no date.

No. 2460, 2 juveniles in *alderi* stage—no date.

No. 3390, 1 ♂, total length 550 mm.—no date.

No. 3493, 1 juvenile in the *alderi* stage, from the stomach of *Alepisaurus ferox*.

This species was originally listed as occurring at Madeira in White & Johnson's *Handbook*, but the name was omitted in the second edition (1885). Subsequent authors have not recorded new material, so that evidence of its occurrence at Madeira was needed. The new records given above dispel this doubt and confirm its presence at Madeira.

Octopus sp.

Material seen :

No. 2960, 1 partly-digested specimen with a total length of 120 mm., from the stomach of *Alepisaurus ferox*, March–April, 1944.

No. 3504, 1 specimen from stomach of *Conger conger* (L.), 18.vii.1952.

No. 3577, 1 specimen with a dorsal mantle length of 14 mm., from stomach of *Alepisaurus ferox*, 10.xii.1952.

It has not been possible to positively identify these specimens with either of the foregoing species or any other, because of their immaturity and poor condition.

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* From the stomach of *Aphanopus carbo* according to a fish gutter

Family ALLOPOSIDAE

Alloposus mollis Verrill

Material seen:

No. 2460, 1 ♀, total length 115 mm., March–April, 1944.
No. 2960, 1♀, total length 115 mm., stomach of *Alepisaurus ferox*.
No. 3491, 5 ♀, total lengths of 80, 115, 115, 115 and 117 mm., from stomach of *Alepisaurus ferox*, no date.
No. 3494, 1 ♀, total length 175 mm., stomach of *Alepisaurus ferox*, no date.
No. 3804, 1 ♀, total length 115 mm., stomach of *Alepisaurus ferox*, 12.vi.1953.
No. 3848, 1 ♀, total length of 50 mm., stomach of *Alepisaurus ferox*, no date.

This species has not been previously recorded from Madeira, but has been taken at the Azores and other places in the North Atlantic, mainly in proximity to coastal waters. Thore, who plotted its distribution (1949, fig. 69, p. 72), regards it as a cosmopolitan, tropical and sub-tropical coast-loving species.

The series now reported from Madeira are all small females (50–175 mm. in total length, compared with Verrill's specimen of 812 mm.) (Verrill, 1882). The paucity of records of *Alloposus* are noted by Thore, who suggests that either it is a rare animal or is able to evade plankton nets or spends " relatively short periods of its life-cycle in open waters, then soon returning to a life at the bottom, especially on the continental slopes." These new records suggest that the species is by no means as rare as the literature suggests and that we lack the gear to take it in numbers. At the smaller sizes (50–175 mm.) it seems to be a regular item in the diet of *Alepisaurus ferox*.

Family TREMOCTOPODIDAE

Tremoctopus violaceus delle Chiaje

Material seen:

No. 3404, 1 ♀, total length 480 mm.
No. 3406, 1 ♀, total length 510 mm.
No. 3408, 1 ♀, total length 305 mm.

There are no previous records of *Tremoctopus* from Madeira. It is well known from the Mediterranean but records from the North Atlantic are remarkably few (these are summarized by Robson, 1932, and Salisbury, 1953).

Family OCYTHOIDAE

Ocythoe tuberculata Rafinesque

Ocythoë tuberculata, Girard, 1892, p. 218; Robson, 1932, p. 202.
Oxythoë tuberculata Nobre, 1937, p. 4.

Material seen:

1 ♀, British Museum, No. 1858.3.31.6 (Robson, 1932).
No. 2460, 1 ♀, total length 115 mm. (33 mm. DML), no data.

No. 3440, 1 ♀, dorsal mantle length of 190 mm.—no data.
No. 3441, 1 ♀, dorsal mantle length of 180 mm.—no data.
No. 3492, 1 ♀, dorsal mantle length of 50 mm., from the stomach of *Alepisaurus ferox.*
No. 3848, 1 ♀, dorsal mantle length of 12 mm., from the stomach of *Alepisaurus ferox.*

Girard records having seen a specimen of this species in the Museu do Seminário do Funchal and there is another in the British Museum.

There are two large specimens noted here (Nos. 3440 and 3441); They compare favourably in size with one reported by Berry (1916) from California. Large as these are, Robson (1932, p. 205) records having seen one of 280 mm. (DML) at Monaco.

The young ♀ specimen (No. 3492) has a total length of 195 mm., and is remarkably well preserved. The tubercules, connected by ridges, on the ventral side of the mantle, are well developed and the aquiferous pores prominent. In another, even smaller specimen (No. 2460), these characteristics are easily seen.

Ocythoë tuberculata is another cosmopolitan species in tropical and sub-tropical waters of all oceans; as far as we know, it is essentially a species which frequents the surface layers. Bouxin & Legendre (1936, p. p. 31) found it in the stomach of the germon in the Bay of Biscay, while Joubin (1900, p. 26) reported three females from the stomach of *Grampus griseus* taken off Monaco.

It is now recorded for the first time as an item in the diet of *Alepisaurus ferox.*

Family ARGONAUTIDAE

Argonauta argo L.

Argonauta argo, Girard, 1892, p. 218; Hoyle, 1885, p. 69; Watson, 1897, p. 274; Nobre, 1937, p. 5.

Material seen:

No. 3489, 1 juvenile ♀, dorsal mantle length 37 mm., no data.

Early records from Madeira and Porto Santo are noted by Girard and Hoyle respectively, and it is not surprising that this cosmopolitan, warm-water species should be found here.

A juvenile female (without shell) is provisionally referred to this species. Watson (1897, p. 274) records one perfect specimen from Porto Santo, and by this we assume (as he was a conchologist) a shell or brood chamber.

Females of about 20–100 mm. in dorsal mantle length are found in great quantities in the stomachs of *Alepisaurus ferox* at Madeira during the months of March, April and May. There is one record for February and another of a single specimen in November. The shells are usually crushed, but sometimes they are quite intact. Eggs have been seen in shells of not more than 50 mm. in diameter. There is, in addition, a single record of a small female (of about 35 mm. in shell diameter) caught in Funchal Harbour at night. Large empty shells are not uncommonly found washed up on the beach of Porto Santo.

IV. AN ANALYSIS OF THE CEPHALOPOD-FAUNA

Surrounded as it is by deep water, the Madeiran Archipelago has a composite fauna with elements from different habitats. In general, the fauna may be said to be a Mediterranean-Atlantic one, which we group as follows :

1. *The coastal fauna*

This includes both littoral and continental shelf species, viz : *Sepia officinalis, Sepietta oweniana, Loligo vulgaris, Loligo forbesi, Todarodes sagittatus, Octopus vulgaris* and *O. macropus.*

All these are common also in the Mediterranean and eastern Atlantic. Only the two species of *Octopus* have a wider distribution in the Atlantic and elsewhere.

2. *The benthic slope fauna*

No Madeiran representatives of this fauna have yet been taken. The deep-water octopods of the genus *Bathypolypus* are typical examples of species found on the bottom below the 200 m. line.

3. *The bathypelagic slope fauna*

In the grouping of these species we are on less sure ground because of the scarcity of locality and depth records. Despite this we believe that the normal habitat of the adults of the species enumerated below is close to the bottom on the continental slope below the 200 m. line, with a lower limit perhaps at 2,000 m.

Spirula spirula.
Lepidoteuthis grimaldi.
Cucioteuthis unguiculata.
Tetronychoteuthis dussumieri.
Architeuthis sp.
Histioteuthis bonelliana.
Ommastrephes pteropus.

4. *The pelagic surface fauna*

By these we mean the species that are habitually found on or very close to the surface. They include :

Ommastrephes pteropus (juveniles).
Onychoteuthis banksi.
Tremoctopus violaceus.
Ocythoë tuberculata.
Argonauta argo.

And possibly also
Thysanoteuthis rhombus.

5. *The epipelagic fauna*

In grouping pelagic forms we have to remember that many species have epipelagic larvae while the adults may live well below the threshold of light. Upwelling from deep water on some coasts and near oceanic islands sometimes brings characteristically deep-water species to the surface and it is not always possible to reach positive conclusions.

The following oceanic species appear to live in the upper 500 metres:

Heteroteuthis dispar.
Abralia veranyi.
? *Enoploteuthis leptura.*
Pyroteuthis margaritifera.
Chiroteuthis veranyi (? juveniles only).
Leachia cyclura (juveniles).
Cranchia scabra.
Japetella diaphana (juveniles).
Alloposus mollis (some part of its life history).

6. *The oceanic bathypelagic fauna*

These include deep-water species which live at or below the threshold of light (*ca.* 700 m.) and which are not confined to the immediate vicinity of the continental slope. These species often have larvae which are epipelagic.

Chiroteuthis veranyi (adult).
Mastigoteuthis schmidti.
Leachia cyclura (adult).
Taonius pavo.
Japetella diaphana.
Eledonella pygmaea.
Vitreledonella richardi.

We think that the occurrence of these species in the Madeiran list is probably due to the fact that there is upwelling which brings them into the upper waters or into the hunting grounds of *Alepisaurus.*

7. *The abyssal fauna*

Truly abyssal forms like *Vampyroteuthis infernalis* Chun have not been taken at Madeira.

In drawing up these lists we have paid but little attention to early records made with open nets from deep water. All too often when a plankton haul has been made with an open net from great depths (say 3,000 m.) to the surface, the resulting catch is reported as from 3,000 metres.

It has been clear for some time, too, that among the Cephalopods, larvae and adults do not always have the same vertical distribution, so that an animal may be a temporary inhabitant of several distinct faunal zones during the course of its life history. Concerning vertical migration or diurnal rhythms in Cephalopods, we have no evidence, nor do we know how tolerant they are of changes in salinity. We do know, however, that some species are sensitive to changes in temperature and that a rapid lowering of temperature by two or three degrees is sufficient to kill some forms (e.g. *Architeuthis* and *Sepia officinalis*).

The above is in broad outline a reasonable grouping of the species, but more exact limits may be possible when we know much more about this group. It must be admitted, for instance, that it is not easy to decide whether the distinction between a bathypelagic slope fauna and an oceanic bathypelagic fauna can be maintained.

As the Madeiran Archipelago is the nearest oceanic group of islands to the Mediterranean, it may be pertinent to note that the following species in the list do not occur there :

Slope animals.

Spirula spirula.
Lepidoteuthis grimaldi
Cucioteuthis unguiculata.
Enoploteuthis leptura.
Tetronychoteuthis dussumieri.
Architeuthis spp.

Bathypelagic species.

Mastigoteuthis schmidti.
? *Leachia cyclura.*
Taonius cymoctypus.
Taonius pavo.
Cranchia scabra.
Japetella diaphana.[1]
Eledonella pygmaea.
Vitreledonella richardi.

Only two of the species, which may be termed slope and bathypelagic species, *Histioteuthis bonelliana* and *Chiroteuthis veranyi*, are found, and are known to breed, in the western Mediterranean. In this area the chief captures have been reported from places like Villefranche-sur-mer and Messina, that is, where upwelling from deep waters occurs.

It is inappropriate here to discuss the cephalopods of the Mediterranean fauna at length, but it can be said that it is poor in bathypelagic species ; this is in agreement with what is known concerning the paucity of deep water species of other groups of animals (Ekman, 1953, p. 369).

V. CEPHALOPODA AS FOOD OF *ALEPISAURUS FEROX*

Alepisaurus ferox Lowe is well known as a voracious fish, and it has been known as a predator on squid since Verrill (1880, p. 234) described a brachial crown of *Histioteuthis* from a fish captured off Nova Scotia in 1879.

Examination of this series of 260 stomachs from Madeiran fishing grounds has yielded many comparatively rare species of squids which are not normally captured by plankton nets. The total of 18 species demonstrates that cephalopods can be regarded as regular items in the diet of this fish :

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[1] " Dana " St. 1132, 36°, 10′ N., 2° 46′ W. in the Western Mediterranean near Gibraltar did yield one larval *diaphana* of 12 mm. (Thore, 1949, p. 28). We concur with Thore that this juvenile specimen was probably swept in through the Straits of Gibraltar in the easterly surface current.

LIST OF SPECIES EATEN

Species.	Total number.	Max. number in one stomach.	Number of stomachs containing cephalopods.	D.M.L.
Heteroteuthis dispar	8	4	4	8–29
Loligo vulgaris	1	1	1	7
Abraliopsis morisii	6	6	1	8–25
Pyroteuthis margaritifera	2	2	1	35
Onychoteuthis banksi	6	4	3	10–48
Todarodes sagittatus	3	1	3	83–86
Ommastrephes pteropus	1	1	1	50
Ommastrephids	5	3	3	17–65
Leachia cyclura	2	1	2	23–50
Cranchia scabra	2	1	2	39–40
Taonius pavo	1	1	1	275
Japetella diaphana	13	4	8	50–85
Eledonella pygmaea	1	1	1	90
Octopus macropus	1	1	1	22
Octopus sp.	1	1	1	15
Alloposus mollis	9	5	5	30–40
Ocythoë tuberculata	2	1	2	12–50
Argonauta argo (see text)				20–100

The dorsal mantle length has been taken as a standard measurement for size, and as a rough guide this is about half the total length of the animal in compact species like *Heteroteuthis dispar, Abraliopsis morisii, Pyroteuthis margaritifera, Cranchia scabra, Japetella diaphana, Eledonella pygmaea, Alloposus* and *Ocythoë.* It represents about only a third of that of *Histioteuthis bonelliana,* where the body is small and the arms disproportionately large. In the long and typical squids like *Loligo, Onychoteuthis, Todarodes, Leachia* and *Taonius,* mantle length is usually more than half the total length.

Japetella diaphana, Alloposus mollis and *Heteroteuthis dispar* are the species most frequently represented and are perhaps rather sluggish creatures. It is particularly noticeable that among the swift-moving species the specimens of *Onychoteuthis banksi* were rather small, several being still in the planktonic stage.

As will have been noted already, none of the cephalopods from the stomach of this fish can be regarded as truly deep-water species in the sense that this term can be applied to forms like *Vampyroteuthis infernalis.* All might reasonably be expected to occur in the upper 200 metres—the depth at which the fish were caught.

Of the eighteen species, only four, namely *Loligo vulgaris, Todarodes sagittatus, Japetella diaphana, Octopus macropus* and *Argonauta argo* are common species in collections. Of the remainder there is little doubt that they are also common species, although records of capture are few. It is only recently that *Japetella diaphana* has been demonstrated to be one of the most abundant pelagic species of cephalopod (Thore, 1949), and Joubin (1933, p. 41) has similarly indicated from a preliminary examination of the " Dana " collections that the Cranchiidae (to which *Leachia* *cyclura, Cranchia scabra* and *Taonius pavo* belong) are also very numerous. Records of *Ocythoë tuberculata* (and possibly also *Alloposus mollis* to a lesser degree) are very few and do not imply scarcity but rather that the fishing gear hitherto employed by expeditions is unsuitable for capturing animals of this group. The same difficulty applies to the capture of swift surface species like *Onychoteuthis banksi* (Rees, 1949).

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NOTES ON THE EUROPEAN SPECIES OF *ELEDONE*

WITH ESPECIAL REFERENCE TO EGGS AND LARVAE

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SYNOPSIS

The newly hatched larvae of the Lesser Octopus, *Eledone cirrhosa* (Lamarck), are described and figured for the first time from material collected by the Fishery Board for Scotland. Records of eggs and spawning have been brought together and additional ones listed. The eggs and larvae of this species are compared with those of the Mediterranean *E. moschata* and the distribution of both species reviewed. *E. moschata* occurs throughout the Mediterranean and its distribution outside is limited to neighbouring coasts, north and south of the Straits of Gibraltar. The records show that *E. cirrhosa* occurs in the western Mediterranean and along the western coasts of Europe to Iceland, the Faroes and northwards to Trondhjem on the Norwegian coast. The characteristics of the two species are compared.

I. INTRODUCTION

In this paper some new observations are made on the eggs and larvae of the Lesser Octopus (*Eledone cirrhosa* Lamarck) and our previous knowledge of its reproduction and distribution is summarized. Early naturalists confused this species with *Eledone moschata* (Lamarck) and it has been deemed desirable to bring together what is known of the eggs and larvae, as well as the distribution of both species to enable a summary of the differences between the species to be presented.[1]

Although *Eledone cirrhosa* is much more widely distributed in North European waters than the Common Octopus (*Octopus vulgaris* Lamarck), it is surprising that so little is known about its habits and life history. Its morphology and anatomy was the subject of a memoir by Isgrove (1909).

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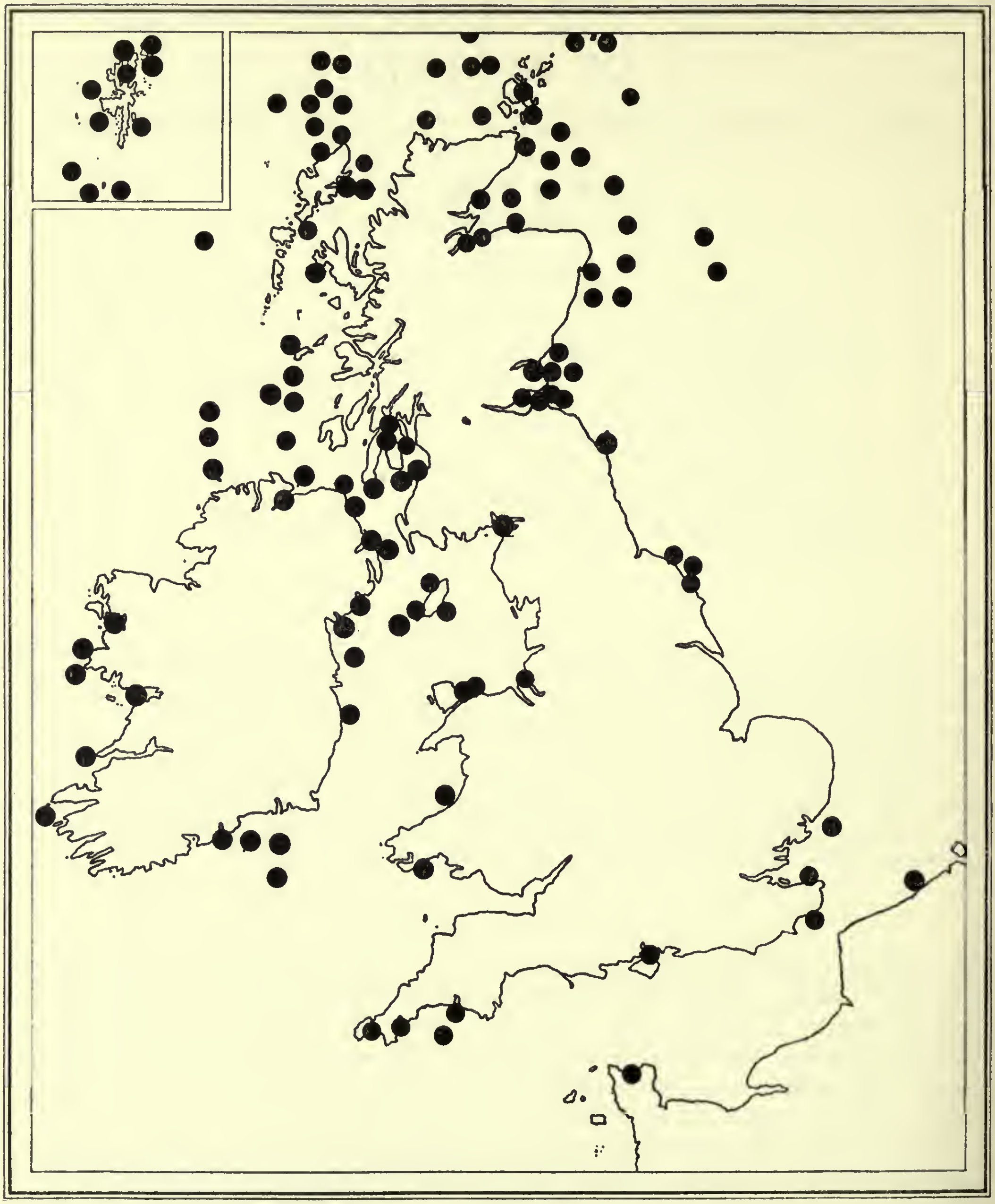
[1] The larva of a South African Eledonid, *Pareledone nigra*, has recently been described by me (see Rees, 1954).



TEXT-FIG. 1.—The recorded distribution of *Eledone cirrhosa* in inshore waters. Trawling records from the central North Sea are not included. The sources of all the records are given in the bibliography.

II. *ELEDONE CIRRHOSA* (LAMARCK)

(a) *Spawning*

The spawning of *Eledone cirrhosa* in captivity was first noted by Joubin (1888) who observed it in an aquarium at Banyuls in the month of June. According to Joubin there were about 30 groups of eggs (and traces of another 30) most of them being eaten by the female. Each bunch contained 5–19 eggs, the greatest number being laid first. The eggs were white in colour, each being 7–8 mm. in length.

Spawning of *Eledone* was also noted by Gravely (1908) in an aquarium tank at Port Erin, Isle of Man, in July. He noted that eggs were about 7 mm. by 2·5 mm. in diameter and that one to four bunches of eggs were laid almost every day for about a month, after which spawning was less regular and was soon over.

Isgrove (1909) states that one *Eledone* lays about 800 eggs and that these are spawned in groups of 25–30 eggs. Egg clusters 4–7 cm. long were collected in Aberdeen market by Bowman ; the full sized ova were 8–9 mm. in length and about 4·0 mm. in diameter at the broad end (Russell, 1922). It now seems that these eggs are a little too large to be those of *E. cirrhosa*, but their identity cannot be known for certain until we have some information on the eggs of *Graneledone verrucosa* (Verrill) ; this species replaces *E. cirrhosa* to the north of the Faroes.

Spawning in aquaria has been noted at Plymouth in January (Marine Biological Association, 1931) and in July (Isgrove, 1909) ; at Port Erin in July (as noted by Gravely) and in September (Moore, 1937, p. 196). A female captured on the Dogger Bank spawned in the Heligoland aquarium in January (Hertling, 1936, p. 294) Stephen (1944, p. 252) mentions several clusters of ova from N.N.W. of Ronas Voe, Shetland (position, 60° 42′ N., 1° 46′ W.) trawled on 4th April, 1927, and, as the embryos were well developed it can be assumed that spawning occurred in February or early March.

From this it appears that *Eledone* may spawn all the year round, and this is borne out by records of larvae, noted by Stephen (1944, p. 251). He observed that although larvae were present all the year in the plankton catches of the Fishery Board for Scotland, they were more frequent during the period May to August ; this suggests maximum spawning in April, May, June and July. As to whether this period of more intensive spawning is linked with the known seasonal migration of *Eledone* into inshore waters we have insufficient evidence. Even the kind of haunt chosen for spawning in nature is not known for certain, but it appears that *Eledone* does not brood over its eggs, nor does it seem to lay them in shells or pots, as does *Octopus vulgaris*, for it has never been taken with its eggs.

(b) *Egg masses*

Apart from eggs seen in aquaria, *Eledone* spawn is rarely taken and only two positive records are known to me, the batches trawled near Ronas Voe in the Shetlands (Stephen, 1944) and a very large cluster from the Eddystone Grounds off Plymouth in the collections of the Plymouth Laboratory.

The large egg mass from the Eddystone Grounds contains a very large number of undeveloped eggs. The stalks of the eggs are very short and the largest eggs are 6·7 mm. in length by 2·4 mm. in width. Some eggs are extremely small, being only 2·85–3·6 mm. in length by 1·0–1·5 mm. in diameter (Pl. 9).

The small egg-cluster from Ronas Voe contains embryos in an advanced stage of development. The eggs themselves are 6·65–6·79 mm. in length by 2·94–3·29 mm. in width. There is still a large yolk mass, but the embryos are well formed. Chromatophores are developing the arms, head and body and the *Köllikersche buschel* are clearly seen on the head and mantle (Pl. 10, figs. 1–4). At this size (3 mm. in. ventral mantle length) the single row of suckers on the subequal arms are formed.

A third cluster in the British Museum is without any particulars; the eggs are poorly preserved and resemble those from Ronas Voe.

Records of larvae of *E. cirrhosa* are few. Lo Bianco (1909) found young *Eledone* in the plankton in the Bay of Naples; those found in April had a length (? total length) of 40 mm. and those found in October a length of 120 mm. He gives no adequate description and there is no certainty as to which species he had. Scottish records of larvae are given by Russell (1922) and Stephen (1944). Russell noted that the arms are much shorter in proportion to the body (3 : 5) in the young, the back is smooth and covered with large chromatophores and the body is generally surrounded by a thick, soft, translucent cuticle.

In the Bay of Biscay area Bouxin and Legendre (1936, p. 24) found seven specimens ranging from 21–33 mm. in length in the stomachs of *germon* in positions approximately 90–100 miles to the south-west of Glenans and at about 250 miles to the south-west (that is, near Cape Finisterre).

A new description is therefore needed and is given below.

(c) *Description of the larvae*

Dr. A. C. Stephen has kindly allowed me to examine a series of 18 larvae, from the catches of the Fishery Board for Scotland, which were reported by him in 1944.

It has already been noted that larvae still in the eggs may reach a ventral mantle length of 3 mm. in large eggs. In small eggs this length would presumably be less, so that planktonic larvae of approximately this size can be regarded as having been taken within a few days of hatching.

The young larva (Pl. 10, figs. 5–6) has much the same shape as the larva of *Octopus vulgaris* (the only species it could be confused with in British waters) with its short arms and rather squat mantle. In details, however, there are big differences, the most noticeable feature being the arrangement of the chromatophores on the mantle. Here the entire mantle is uniformly covered with large reddish brown chromatophores, and these are also prominent on the head and arms. On the latter there is a single row and those of the central portion of the head are deep-seated. Overlying these in the transparent outer integument are other fainter reddish brown chromatophores, which increase in number and size with growth. The outer integument of the eye is silvery and sometimes has a greenish hue.[1]

The arms are subequal and do not have the thin cirriform tips seen in very young larvae of *Octopus vulgaris*. No. 12 (Table I) has 6–7 fully formed suckers on each arm with the clear rudiments of 8–9 more at the tip of the arm. A slightly larger specimen (No. 13) has 9 suckers on each arm and about 8 rudiments at the tip.

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[1] All references to colour mean colour of preserved specimens in alcohol.

The largest larva available (No. 19) has about 28 suckers plus rudiments at the tip. The first proximal sucker has a diameter of 0·56, the second, third and fourth have a diameter of 0·7, 0·84 and 1·05 respectively. Suckers 5–7 are the largest and then they diminish in size distally. The web is subequal reaching to the 7th–8th suckers, that is, to about one-third of the length of the tentacles. This specimen taken on 27th November, 1930, was recorded from square E 13 b by Stephen (1944).

This late larva has developed a mantle fin-ridge as in the adult. The ventral mantle is smooth but the dorsal mantle and head are both covered with tubercles. The larval chromatophores are still discernible because of their large size, but the areas in between have become covered with a large number of small chromatophores.

As noted above, the arms of the larval *Eledone* are quite short at hatching from the egg and they are usually not so long as the ventral mantle (Table I). Growth of the arms of the planktonic larvae is more rapid than mantle length (Figs. 3 and 4) and is also reflected in the relation of mantle length to total length (Fig. 2).

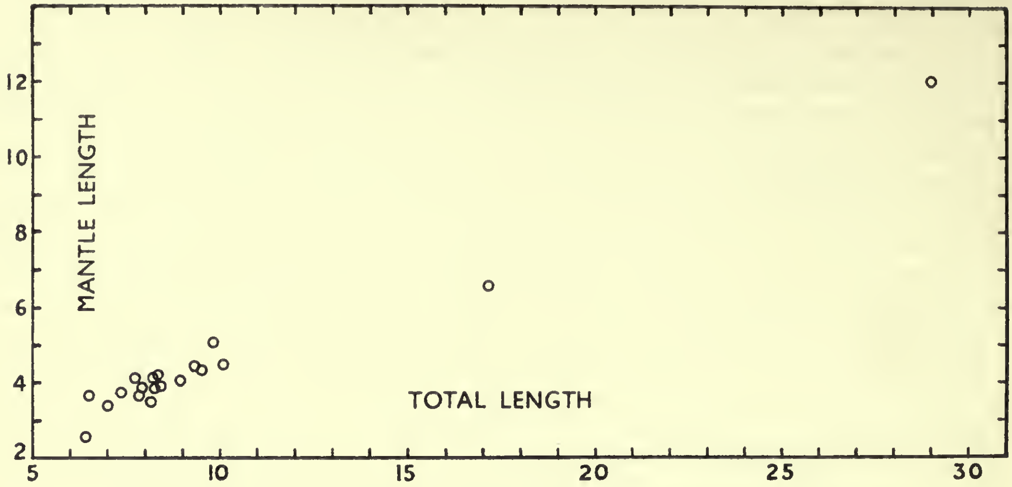
TABLE I.—*Larvae Collected by the Fishery Board for Scotland*

	No.																		
	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.	12.	13.	14.	15.	16.	17.	18.	19.
Total length	6·5	7·0	6·45	7·9	8·95	8·25	8·2	8·12	8·34	7·84	8·4	7·35	9·31	10·08	7·7	9·45	9·87	17·15	29·0
Dorsal mantle length (to eye)	3·9	4·2	3·85	4·2	4·9	4·7	4·83	4·4	5·05	4·55	4·97	4·62	5·11	5·39	4·76	5·25	5·95	7·7	13·0
Ventral mantle length	3·65	3·35	2·52	3·85	4·06	3·85	4·06	3·43	4·2	3·64	3·92	3·71	4·41	4·48	4·06	4·34	5·04	6·58	12·0
Head width	2·8	3·0	2·8	3·5	3·55	3·5	3·57	3·5	3·43	3·5	3·5	3·71	3·99	4·55	3·78	4·13	4·2	6·3	9·0
Mantle width	3·15	3·2	3·55	3·85	3·78	3·64	4·4	3·99	3·64	4·2	3·85	4·06	4·62	4·9	4·2	4·76	4·69	7·14	10·0
Diameter of eye	0·8	1·05	1·05	1·05	1·1	1·2	1·2	1·26	1·05	1·4	1·26	1·26	1·4	1·4	1·3	1·6	1·5	2·2	3·5
Length of arms	2·45	2·8	2·5	3·08	3·5	3·15	3·15	3·15	2·8	2·8	3·22	2·66	3·71	3·92	2·94	3·85	3·8	8·4	16·0
Diameter of suckers	0·2	0·3	0·22	0·32	0·3	0·38	0·34	0·3	0·38	0·32	0·3	0·32	0·4	0·4	0·3	0·4	0·4	0·7	1·12–1·2

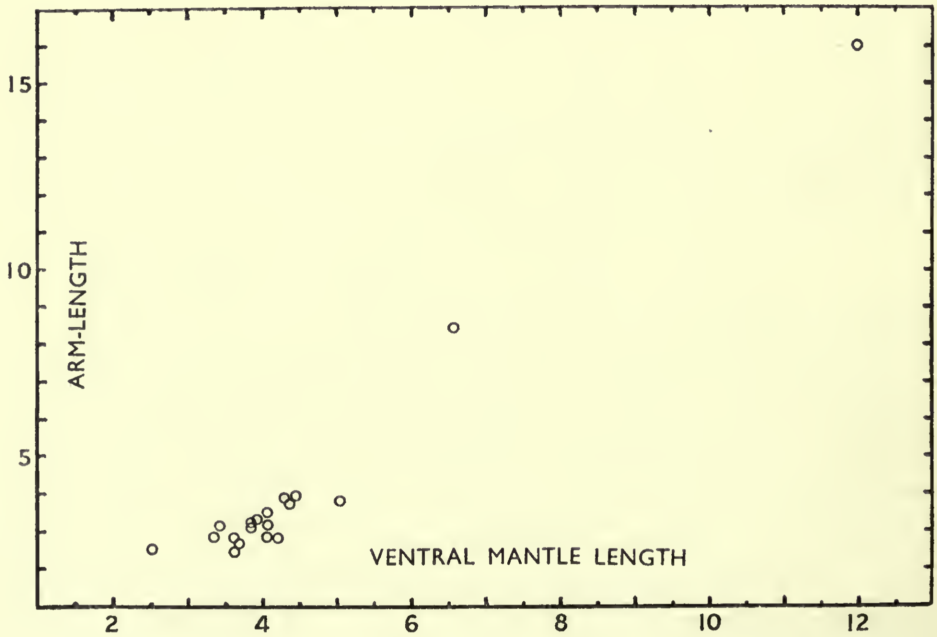
III. *ELEDONE MOSCHATA* (LAMARCK)

(a) *Egg masses and larvae*

We know less about the spawning and larval stages of this species than we do of *Eledone cirrhosa*. Korschelt (1893) described an egg-mass found on a *Pinna* shell at



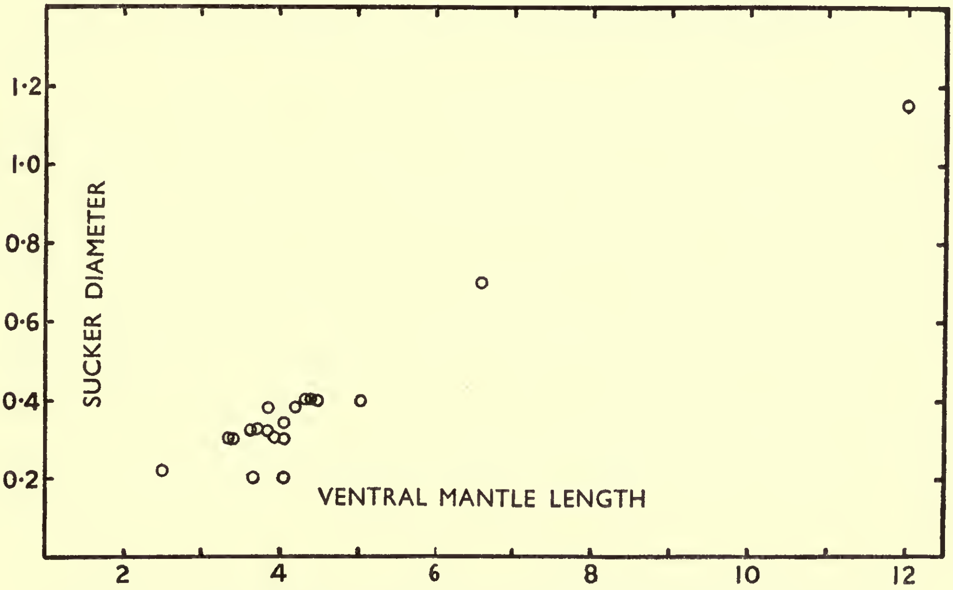
TEXT-FIG. 2.—The relation of mantle length to total length in larvae of *Eledone cirrhosa*. Measurements are in mm.



TEXT-FIG. 3.—The relation of arm length to ventral mantle length in larvae of *Eledone cirrhosa*. Measurements are in mm.

Rovigno in the Adriatic. He gave the total number of eggs as 65–70; this mass was made up of small clusters of 2–4 eggs joined to the main mass by a common stalk. The eggs (excluding stalk) were 15 mm. in length, that is, the same length as the eggs figured by Jatta (1896, tav 7, fig. 3).

Korschelt was under the impression that he had the eggs of *E. aldrovandi* (i.e., *cirrhosa*), but this mistaken view was corrected with the identification of the large eggs with *E. moschata* by Jatta and confirmation by Gravely (1908) that the smaller eggs belonged to *E. cirrhosa*. There have been embryological studies on development in the egg (Sacarrao, 1943, 1945, 1951 and 1952) but there is no detailed description of the newly hatched larva. Sketches of juvenile *Eledone* have been published by Jatta (1896, tav 7, figs. 5 and 10), while Naef (1923) gives a drawing of a post-larval *E. moschata* from Trieste. A new description is much needed.



TEXT-FIG. 4.—The relation of sucker diameter to ventral mantle length in larvae of *Eledone cirrhosa*. Measurements are in mm.

IV. DISTRIBUTION OF THE EUROPEAN SPECIES

Eledone cirrhosa (Lamarck) is found in the Mediterranean, but its full distribution there is not known. It appears to be a common species in the western part, but there are no records for the eastern Mediterranean. Under the name *Eledone aldrovandi* there are numerous records for the western Mediterranean (Jatta, 1896), but there are no records east of Dalmatia (Robson, 1932, p. 266) and according to Ninni (1884) it does not penetrate to the head of the Adriatic.

In the Atlantic *E. cirrhosa* has a much less restricted distribution than *E. moschata*.

It is a common species on the European continental shelf extending to southern Iceland, the Faroes (Brunn, 1945, p. 8) and the west coast of Norway. In the open areas of the shelf it appears not to extend beyond the line Iceland-Faroes-Bergen, but is a common species southwards of this line. On the Norwegian coast itself it reaches Ostnesfjord in the Lofotens, but is said to be scarce north of the Trondhjemsfjord (Grieg, 1933).

Its distribution in inshore British waters as recorded in the literature on cephalopods is plotted on Map I, and, quite apart from the fact that such maps tend to reflect areas worked by biologists, the species appears to be scarcer in the southern North Sea than elsewhere. Records from trawling grounds offshore have not as a rule been plotted (those from the North Sea trawling grounds are given by Grimpe, 1925), and it has not been possible to search for all the occasional records buried in the transactions of local natural history societies.

Eledone moschata (Lamarck) is a Mediterranean species which ranges from Istanbul (Digby, 1949), the Syrian coast (Gruvel, 1931) and Palestine (Bodenheimer, 1937) to the adjoining region of the Atlantic. Korschelt (1893, p. 68) implies that it is the common *Eledone* of the Adriatic and it has also been found commonly at Naples (Jatta, 1896, and Naef, 1923), the Gulf of Marseilles (Vayssière, 1917) and Monaco (Boone, 1933) to quote only a few of the more recent records. Outside the Mediterranean the species appears to be rare and records are few. The " Talisman " took a female specimen in the Bay of Cadiz from a depth of 60 m. (Fischer & Joubin 1907, p. 328), while Adam (1941, p. 140) reported the first specimen from the African Coast (Baie du Levrier, Port-E'tienne, Mauritania).

There are no authentic records from northern Europe ; Nielsen's *Eledone moschata* from the Faroes (1930) proved on re-examination to be *E. cirrhosa* (Brunn, 1945, p. 9).

V. THE DIFFERENCES BETWEEN *ELEDONE CIRRHOSA* AND *E. MOSCHATA*

The main differences between the species are tabulated below.

Eledone cirrhosa	*Eledone moschata*
No musk odour.	Musk odour.
Skin with warts on dorsum.	Skin smooth.
Ridge along edge of mantle.	No pallial ridge.
The seven non-hectocotylized arms of the male carry close-pressed, flattened suckers, forming cirri at the tips of the arms.	The seven non-hectocotylized arms carry a double series of transverse lamellae at their tips.
The two retractor muscles of the gills are fused at their base and form a " Y "	The two retractor muscles of the gills are inserted separately.
Spermatophore with spines.[1]	Spermatophore without spines.
Colour of adult : Light yellowish brown with diffuse rust-brown patches on the back. Ventral mantle pale ivory or pinkish yellow with a greenish iridescent sheen.	Colour of adult : Greyish brown colour with darker almost black patches on the dorsal side. Preserved animal is grey to dark grey with numerous dark patches.
Eggs, Pyriform, *ca.* 7 × 2·5 mm. in clusters of about 30.	Eggs sausage-shaped *ca.* 15 × 4 mm. in clusters of two to four.

[1] Fort (1941) creates a new genus *Acantheledone* for *E. cirrhosa* laying particular stress on this character.

Eledone cirrhosa (cont.)	*Eledone moschata* (cont.)
Newly hatched young *ca.* 3·0 mm. in ventral mantle length.	Newly hatched young probably *ca.* 8 mm. in ventral mantle length.
Parasites :	*Parasites :*
Dicyemennea eledones (Wagner, 1857).	*D. eledones.*
Chromidina coronata (Foettinger, 1881).	*D. moschatum* Whitman, 1882.

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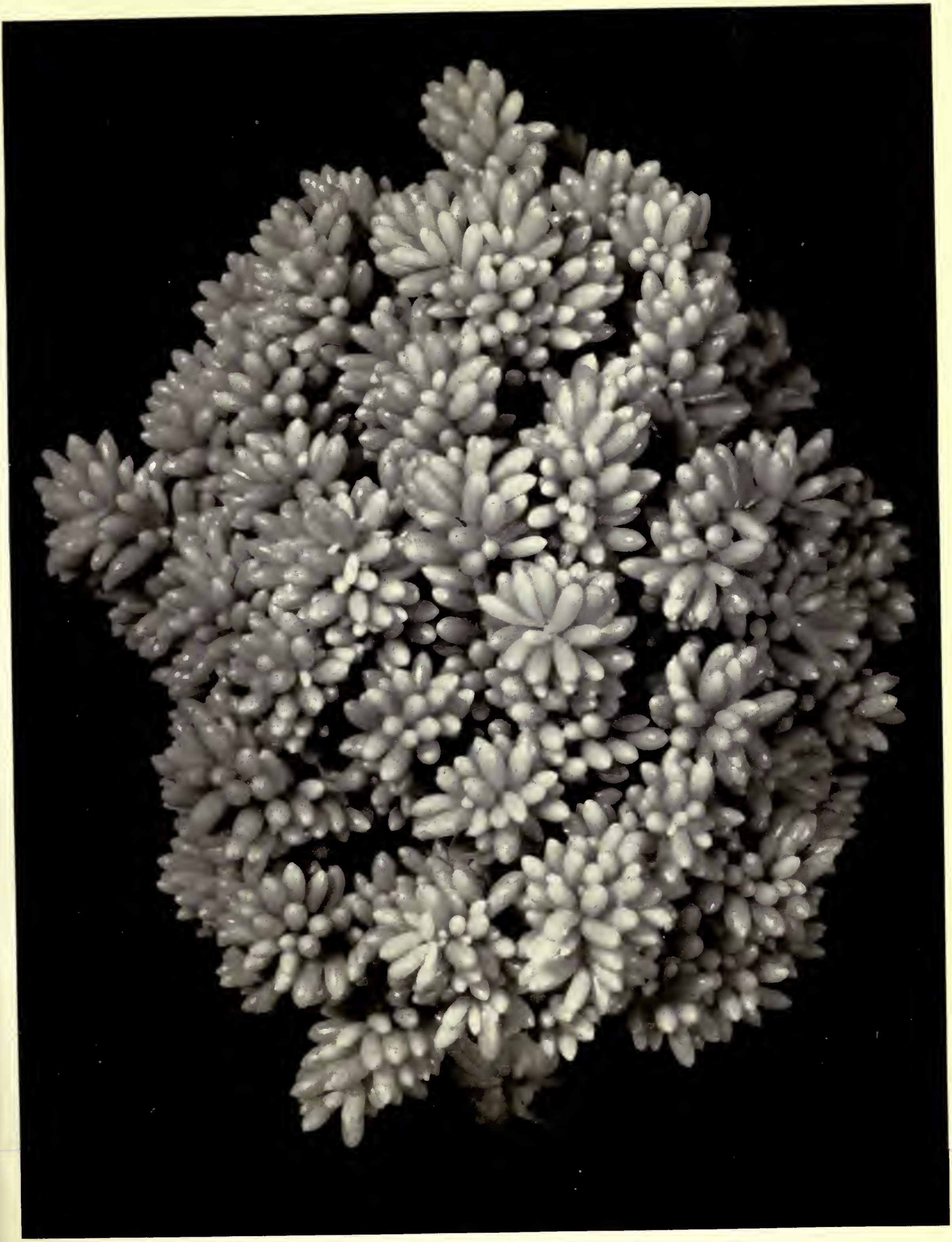
EXPLANATION OF PLATES

PLATE 9

Egg mass of *Eledone cirrhosa* (Lamarck) from the Eddystone Grounds, Plymouth.



Egg mass of *Eledone cirrhosa* (Lamarck)

PLATE 10

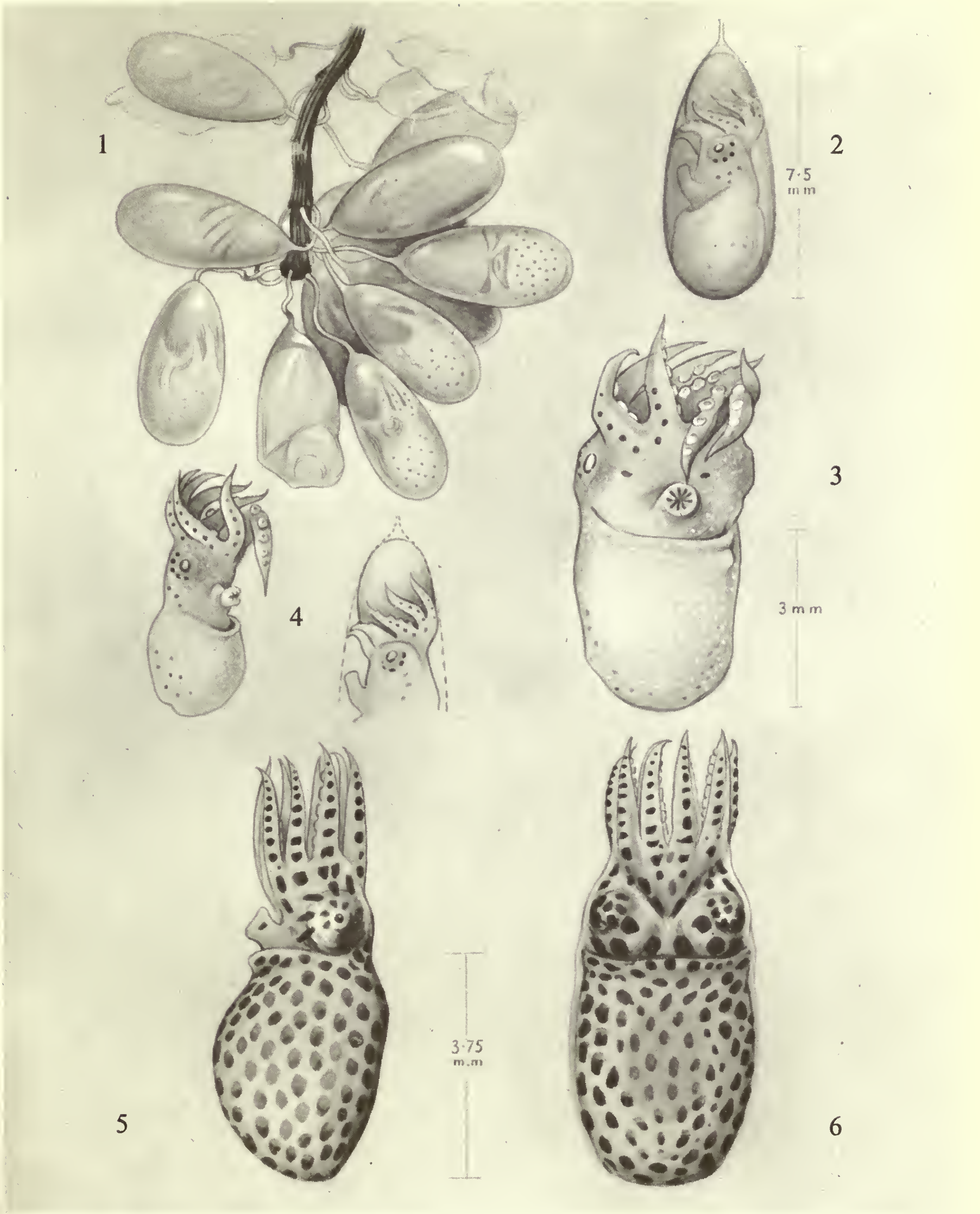
Eggs and larvae of *Eledone cirrhosa* (Lamarck) del. G. L. Wilkins.

FIG. 1.—Portion of an egg cluster from Ronas Voe, Shetlands.

FIG. 2.—A well developed larva *in situ*.

FIG. 3–4.—Views of larvae removed from their egg capsules.

FIG. 5–6.—Side and ventral views of a planktonic larva from the catches of the Fishery Board for Scotland.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Eggs and larvae of *Eledone cirrhosa* (Lamarck)

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BY

P. H. GREENWOOD

(East African Fisheries Research Organization, Jinja, Uganda)

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THE MONOTYPIC GENERA OF CICHLID FISHES IN LAKE VICTORIA

By P. H. GREENWOOD, B.Sc.

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INTRODUCTION

In his revision of the Lake Victoria Cichlidae, Regan (1922) recognized four endemic monotypic genera, the species being *Astatoreochromis alluaudi* Pellegrin, 1904, *Hoplotilapia retrodens* Hilgendorf, 1888, *Platytaeniodus degeni* Boulenger, 1906, and *Macropleurodus bicolor* (Boulenger), 1906. Subsequent collections made by the Cambridge Expedition (1930–1931) extended the range of *A. alluaudi* to include the Lake Edward system and Lakes Kachira and Nakavali (Trewavas, 1933), but provided no further distributional data for the other three genera. Since *Astatoreochromis alluaudi* occurs beyond the Victoria system, it is preferable to delay revision of this species until numerous specimens from the different localities can be examined. Some notes on the osteology and possible phyletic relationships of *Astatoreochromis* have been published already (Greenwood, 1954).

A fifth genus which, but for its geographical separation, would not have been distinguished from *Labidochromis* of Lake Nyasa, is recorded for the first time.

The present study is based on specimens collected by and for the East African Fisheries Research Organization during a field study of the Lake Victoria Cichlidae, and on material in the collections of the British Museum (Nat. Hist.), Muséum National d'Histoire naturelle, Paris, and the Museo Civico di Storia Naturale, Genoa. It forms the first part of a revision of the Lake Victoria *Haplochromis* species flock.

Notes on counts and measurements

The counts and measurements used are as defined by Trewavas (1935), except that " length of head " is measured directly from the posterior margin of the operculum to the premaxillary symphysis. This method has been found to yield more consistent results than measurements taken between verticals through the posterior tip of the operculum and the *level* of the tip of the snout, along a line parallel to the longitudinal axis of the body. Likewise, length of snout is measured directly.
Other measurements and counts are :

Depth of preorbital : measured from about the middle of the orbital rim of the preorbital bone along a line which continues the radius of the eye at this point ; the line approximately bisects the bone.

Interorbital width : the least width of the roofing part of the frontal bones, between the eyes.

Lower jaw : measured directly from the angle to the symphysis.

Lateral line scale series : After last upper lateral line scale, proceed to the scale of the lower lateral line next behind the transverse row that includes the last scale of the upper lateral line and slopes downwards and forwards from it.

In addition to those defined by Trewavas. Depth of cheek : the greatest depth measured vertically from the lower orbital margin to the lower edge of the *adductor mandibulae* muscles. In most specimens this is virtually a measurement of the depth of the scaled portion of the cheek.

Post-ocular part of the head: measured directly from the posterior orbital margin to the posterior tip of the operculum.

SYNOPSIS OF GENERA OF THE HAPLOCHROMIS GROUP OCCURRING IN LAKE VICTORIA

1. Anal spines three . . . . 2.
   Anal spines four or more . . . . *Astatoreochromis*
2. Teeth of upper jaw in two or more series anteriorly, but only in a single (rarely double) series laterally . . . . 3.
   Teeth of upper jaw in 2–5 series both anteriorly and laterally . . . . . 4.
3. Anterior outer teeth disproportionately longer than the adjacent lateral teeth, slender, unicuspid and procurrent. . . *Paralabidochromis* gen. nov., p. 327
   Anterior outer teeth forming a graded series with the lateral teeth, not forwardly directed . . . . *Haplochromis*
4. Outer teeth enlarged and stout, with obliquely truncated and inwardly directed crowns . . . . *Macropleurodus*, p. 299
   Outer teeth of both jaws small, bi- or unicuspid; inner teeth in broad bands anteriorly and laterally . . . . 5.
5. Lower jaw broad and flat, tooth bands in both jaws of uniform breadth anteroposteriorly; those of lower jaw continued posteriorly on to the ascending part of the dentary . . . . *Hoplotilapia*, p. 319
   Lower jaw stout, rounded anteriorly; teeth aggregated anteriorly into two pyriform bands, contiguous at the symphysis . . . . *Platytaeniodus*, p. 312

Genus *MACROPLEURODUS* Regan, 1922

Bayonia Boulenger, 1911 (*nec*. Bocage 1865), type species *Bayonia xenodonta* Blgr.
Macropleurodus Regan, 1922, Proc. zool. Soc., Lond. 189; type species: *Haplochromis bicolor* Boulenger, 1906, Ann. Mag. nat. Hist. (7) **17**, 444.
Haplochromis (part)
Paratilapia (part) } For references see synonymy under species.
Hemitilapia (part)

Generic characters and synonymy

Prior to Regan's revision of the Lake Victoria Cichlidae (Regan, 1922) specimens of the genus here recognized as *Macropleurodus* had been described as belonging to several genera and species. When Regan (*op. cit.*) defined the apparently new genus, *Macropleurodus* he did not have at his disposal specimens covering the wide range necessary to determine ontogenetic changes in certain characters. Consequently he failed to recognize that his genus was identical with Boulenger's *Bayonia* (Boulenger, 1911), and incorrectly assigned the type specimens of this and one other synonymous "species" to *Haplochromis*.

Regan's diagnosis of *Macropleurodus* gave particular emphasis to the posterior premaxillary teeth:

" . . . several inner series of small teeth anteriorly and three or four series of enlarged teeth laterally, which are exposed when the mouth is shut" (Regan, 1922).

The two specimens on which this description was based have the posterolateral inner teeth not only enlarged, but also similar in form to adjacent outer teeth. It is now known, however, that in small individuals these inner teeth are only slightly enlarged, if at all, and do not closely resemble the outer teeth. Specimens available indicate that most fish between 80 and 90 mm. standard length have a dentition intermediate between juvenile and adult types. In these, many of the typically juvenile, stoutly bi- and unicuspid inner teeth are replaced laterally by teeth differing only slightly in size and form from those of the outer series. Individuals below 80 mm. lack enlarged inner teeth.

Thus, although Regan's diagnosis is incisive for fishes over 90 mm. S.L., it is not sufficiently comprehensive to include smaller individuals.

On the other hand, the present collection shows that the morphology of the outer teeth is equally diagnostic and, moreover, is little affected by the size of the individual. Basically, the outer series is composed of stout teeth, having enlarged and obliquely truncated anterior cusps and disproportionately smaller posterior cusps. In the upper jaw these teeth are implanted obliquely to the long axis of the premaxilla, so that their crowns lie at an angle to it and the anterior cusp points inwards. Teeth of this type are present in all the specimens examined and are not known to occur in any *Haplochromis* or related species.

The peculiar form of the outer teeth in *Macropleurodus* at once suggests affinity with *Bayonia xenodonta* Boulenger (1911), in which the outer teeth are described as having " . . . very large compressed crowns, with long anterior cusp directed inwards and very short or indistinct posterior cusp . . . ". In this respect, the published figure of *B. xenodonta* (Boulenger, 1911 and 1914) is somewhat misleading since the teeth are stouter than depicted.

Through the courtesy of Dr. D. Guiglia, re-examination of the type specimen of *B. xenodonta* has been possible and has confirmed that the outer teeth are alike in *Bayonia* and *Macropleurodus*. Further, as Regan and Trewavas (1928) first observed, Boulenger's description of the inner teeth is inaccurate. Posteriorly these teeth form a double series, with six teeth on either side nearly as large as the outer, and in this respect conform to the dental pattern of young *Macropleurodus*. Also, the more anterior teeth of the two inner series are not " minute and conical " but are in fact tricuspid. Thickening of the buccal mucosa (probably a fixation artefact) has buried the inner teeth so that only their major cusps protrude. Two types of tricuspid teeth are present : one, the usual small tricuspid tooth found in many species of *Haplochromis* ; the other, stout and with the minor cusps displaced so as to form a triangular crown having the major cusp at its apex. Similar trigonid teeth are also found in *Macropleurodus*, both young and adult, but have not been observed in *Haplochromis*.

There is also agreement in morphometric characters and, although *Bayonia xenodonta* has only twenty-four outer teeth in the upper jaw, this number is within the known lower range for *Macropleurodus* (see below).

There seems little doubt, therefore, that in all salient features the type and unique specimen of *Bayonia xenodonta* is identical with small specimens of *Macropleurodus bicolor*, and that the two are conspecific.

One other name has been given to cichlid fishes from Lake Victoria with teeth of the *Macropleurodus* type, namely *Hemitilapia materfamilias* Pellegrin, 1913. I have examined the holotype (no. 12.278 in the collection of the Muséum d'Histoire naturelle, Paris) and found it to agree closely with *Macropleurodus* of similar size. The teeth and dental pattern of the type and three other specimens represent an advanced stage in the transition from juvenile to adult condition; that is, the postero-lateral premaxillary teeth of the first inner series are nearly comparable in size and form with the adjacent outer teeth. The remaining inner teeth are small and unequally bicuspid.

Regan (1922) tentatively synonymized *H. materfamilias* with *Haplochromis obliquidens* Hilgendorf; apparently he did not examine the type of *H. materfamilias* (*op. cit.*, pp. 157 and 158) and was misled by Pellegrin's description. Comparison of the holotype with specimens of *H. obliquidens* at once reveals the existence of fundamental differences in the dentition of the two species. In *H. obliquidens* the movably implanted outer teeth are fine and numerous (50–70 in upper jaw); the posterior cusp is wanting, except very occasionally in small fish, whilst the anterior cusp, although obliquely truncate, is compressed and slender. In contradistinction, the immovable outer teeth of *H. materfamilias* are coarse and less numerous (24–40); with few exceptions a posterior cusp is present and the stout anterior cusp is circular in cross section.

Diagnosis

Cichlid fishes of the *Haplochromis* group as defined by Regan (1920, 1922) but differing from *Haplochromis* in having stout outer teeth with inwardly directed and obliquely truncated crowns; anterior cusp long, slightly decurved and not compressed, the posterior cusp small and indistinct. Fishes over 90 mm. S.L. have one or more inner premaxillary tooth-series composed laterally of enlarged teeth similar in form to the adjacent outer teeth. Consequent upon the enlargement of the lateral teeth, the dentigerous surface of the premaxilla is broader laterally than anteriorly. In small individuals, where the inner teeth are small and bi- or unicuspid throughout the series, the outer teeth are already characteristic. Teeth usually exposed laterally, even when the mouth is shut.

Macropleurodus bicolor (Boulenger) 1906

(Fig. 1)

Haplochromis bicolor (part) Blgr. 1906, Ann. Mag. nat. Hist. (7) **17**, 444 (type only).

Paratilapia bicolor (part) Blgr. 1907, Fish. Nile 479, pl. lxxxix, fig. 1; *Idem*, 1911, Ann. Mus. Genova (3) **5**, 68; *Idem*, 1915, Cat. Afr. Fish. **3**, 346, fig. 234.

Bayonia xenodonta Blgr. 1911, Ann. Mus. Genova (3) **5**, 70; *Idem*, 1915, *op. cit.*, 488, fig. 338.

Hemitilapia materfamilias Pellegrin, 1913, Bull. Soc. zool. France, **37**, 313; Boulenger, 1915, *op. cit.*, 492.

Haplochromis obliquidens (part), Regan 1922, Proc. zool. Soc., London, 188.

Macropleurodus bicolor, Regan, 1922, *op. cit.*, 189.

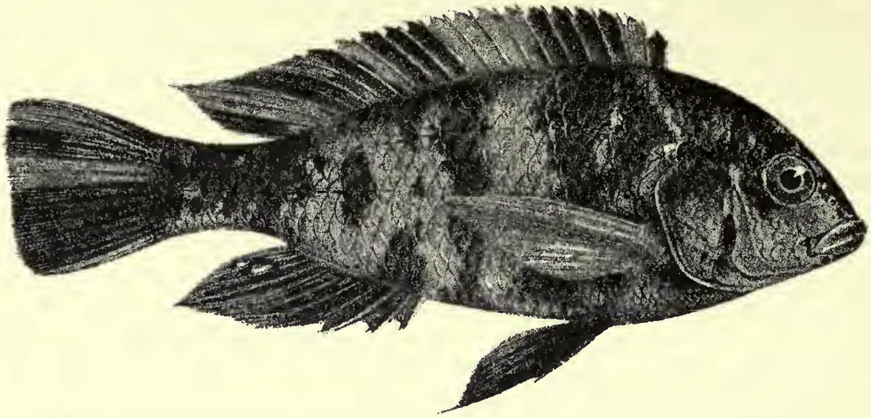
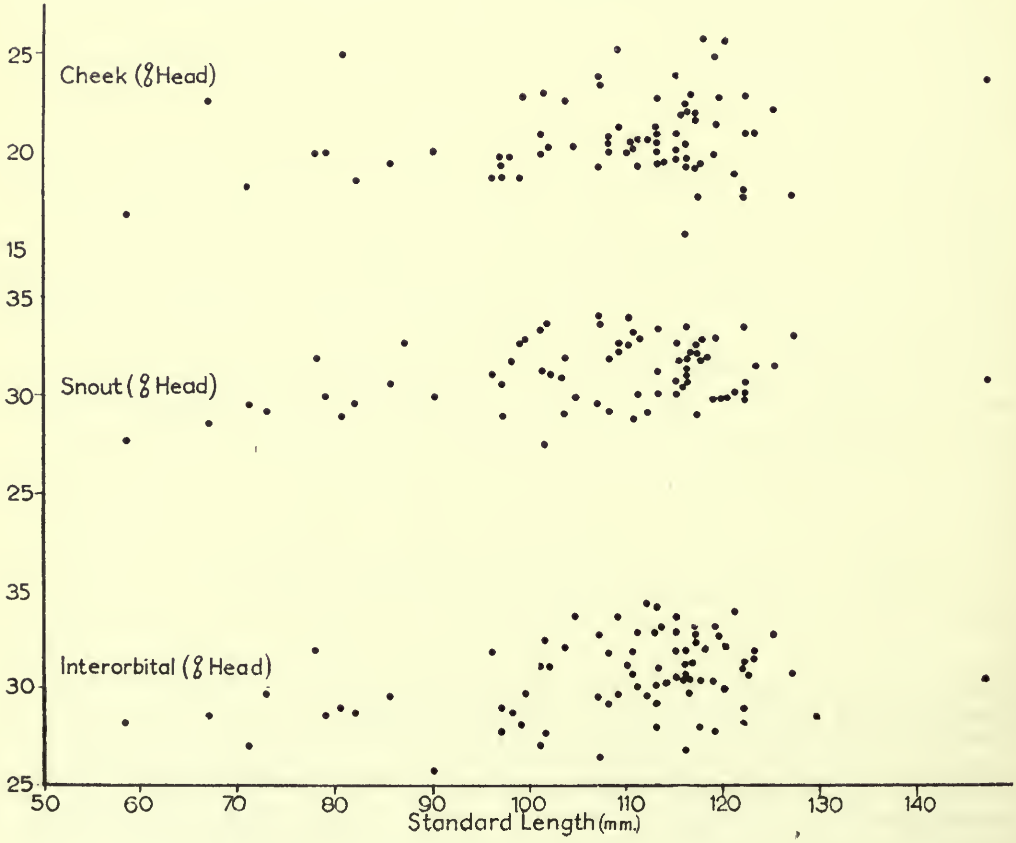


FIG. 1.—*Macropleurodus bicolor*, holotype. 7/8 N.S. (From Boulenger, *Fishes of the Nile.*)



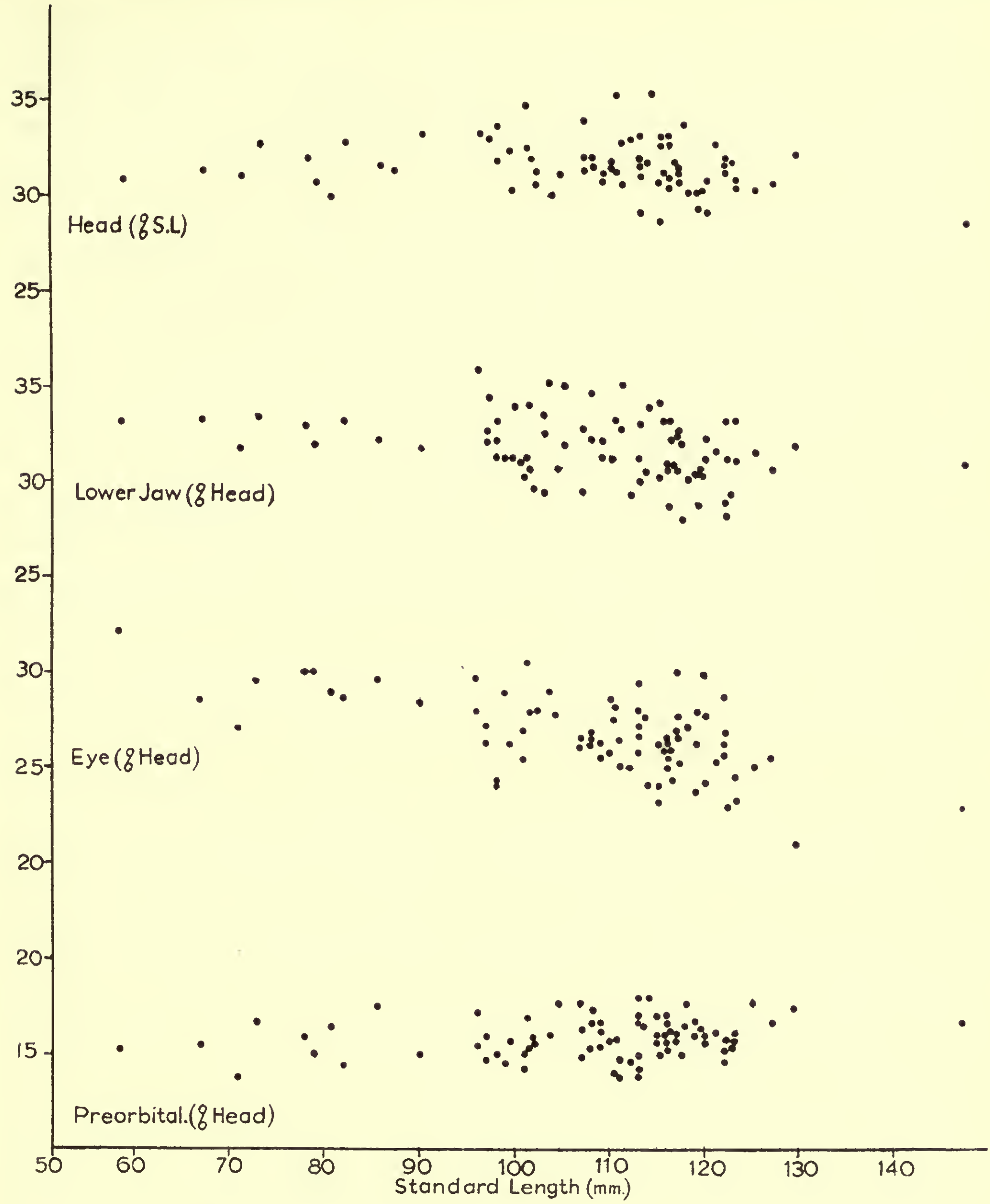


FIG. 2.—Scatter-diagram to show individual variation and allometry of the characters indicated. The isometric relationship of head length and standard length is usual, as is the allometry of head length and the inter-related snout, eye and preorbital measurements. The negative allometry between length of lower jaw and head length is unusual and seems to be related to the stronger jaws and enlarged teeth of larger specimens. These diagrams show scatter but not frequency. Within the size-range 100 to 125 mm. S.L., each dot in the denser aggregates represents at least two specimens.

Description

The selectivity of sampling gear used has resulted in a very unequal size distribution of specimens, with a bias towards the larger size groups. Thus subdivision of morphometric data by size groups is not entirely satisfactory; furthermore, there is considerable variation within and overlap between various groups. Despite these limitations, however, most metric characters do show some allometry with standard length (Fig. 2).

Depth of body 34·4–40·8, mean (M)=37·6, length of head 29·0–35·3 (M = 31·7) per cent of standard length. Dorsal profile of head and snout variable, from straight but sloping through decurved to strongly decurved (Fig. 3), without size or sex correlation. Preorbital depth 13·6–18·3 (M = 16·0) per cent of head length; least width of interorbital 25·8–34·5 (M = 30·8); snout length 26·5–34·2 (M = 31·5), eye 21·4–32·0 (M = 27·0), depth of cheek 16·7–26·0 (M = 21·3), length of post-ocular part of head 41·0–50·0 (M = 47·8) per cent of head length. Described from one hundred and one specimens, 60–150 mm. standard length.

Mouth short and broad; maxilla extending to the vertical from the anterior margin of the orbit, or, more frequently, to anterior third of eye. Jaws unequal, lower jaw somewhat shorter than upper, 28·0–36·0 (M = 31·9) per cent of head length, its length/breadth ratio from 1·3 to broader than long, with a mode at unity.

Gill rakers short and stout, lowest one or two reduced; 7–8 (rarely 9 or 10) on lower limb of anterior arch.

Scales ctenoid; lateral line interrupted, with 31 (f.7), 32 (f.36), 33 (f.29), 34 (f.26), or 35 (f.3) scales. Cheek with three or four (rarely two) rows of imbricating scales; 6–8 scales between dorsal fin and lateral line, 7–9 between pectoral and pelvic fin insertions.

Fins. Dorsal with 23 (f.1), 24 (f.13), 25 (f.67), 26 (f.18), or 27 (f.2) rays; anal with 11 (f.7), 12 (f.82), 13 (f.11), or 14 (f.1) rays comprising XIV–XVII 8–11 and III 8–11 spinous and soft rays for the fins respectively. Pectoral fin 25·2–32·0 (M = 28·8) per cent of standard length. Pelvics with the first soft ray produced, variable in its posterior extension, but usually reaching to vent in immature fishes, and as far as the spinous part of the anal fin in adults. Caudal sub-truncate, scaled on the proximal half only.

Teeth. Little remains to be added to the description given above. There are 24–40 outer teeth in the upper jaw (mode 34); the number of teeth shows a weak positive correlation with size, especially in fish less than 100 mm. S.L.

Two variants of the outer teeth are known, neither of which affects their characteristic shape. In one there is developed a double posterior cusp; in the other, the posterior cusp is wanting. As this latter type occurs only in large fishes, it is possible that loss of the smaller cusp may be due to attrition.

Inner tooth bands with 2–4 series anteriorly and laterally, narrowing to 1 or 2 series posteriorly. In contrast to the outer series, inner teeth show considerable variation in form, being tricuspid, or variously bicuspid. Tricuspid teeth with the cusps arranged in triangular outline, occur at all sizes; the type of *Bayonia xenodonta* is exceptional in possessing inner teeth mainly of this type.

There is noticeable asymmetry in the degree to which lateral teeth of all series are enlarged. Most specimens examined show a distinct tendency for the dextral tooth band to be wider and its teeth larger than on the left side. Only a few specimens show symmetrical or sinistral hypertrophy. In both fresh and preserved material the outermost premaxillary teeth are usually exposed laterally even when the mouth is closed, although there is marked variation in the symmetry and degree of exposure. Hypertrophy of lateral teeth on one side is usually associated with a greater exposure of the teeth on that side.

Pharyngeal bone. Triangular, short and broad ; teeth small and cuspidate, the median series often enlarged.

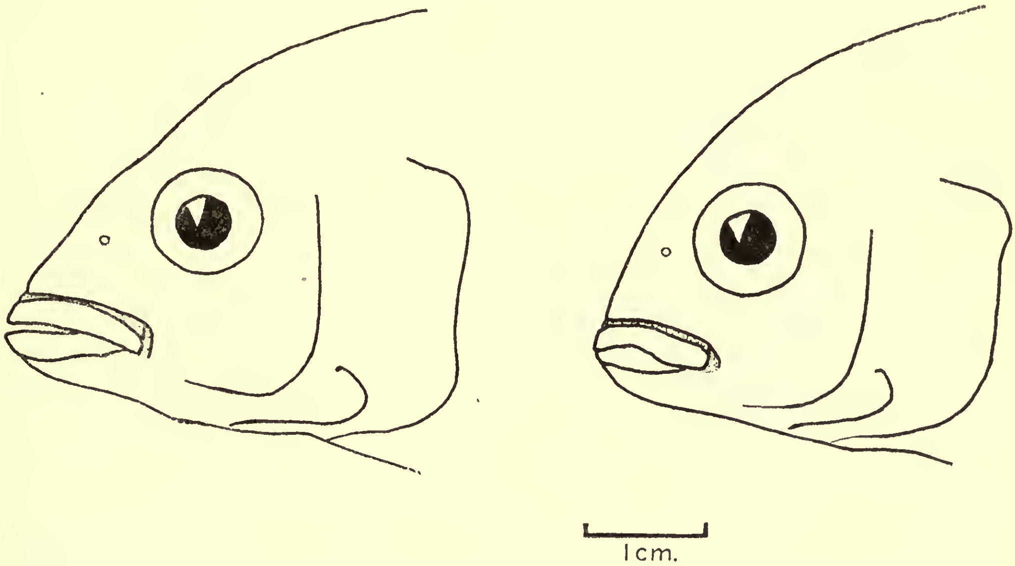


FIG. 3.—*Macropleurodus bicolor.* Individual variability of head profile.

Syncranium and associated musculature

A general impression gained from the syncranium of *Macropleurodus* is one of antero-posterior compression. This is due to the short lower jaw, steeply aligned ethmo-vomerine complex and deep concavity in the entopterygoid, which accommodates part of the short and broad *adductor-mandibulae* muscles.

Both the neurocranium and premaxilla warrant description (Fig. 4). Unpublished observations on skulls of Lake Victoria *Haplochromis* show clearly that the neurocranium of *Macropleurodus* is atypical, although closely paralleled by that of *Haplochromis prodromus* Trewavas, 1935 (= *H. annectens* Regan, 1922, *nec Cyrtocara annectens* Regan, 1921). From the generalised, but common *Haplochromis* skull-type, it differs principally in having a shortened and strongly curved preorbital face, with the anterior profile ascending almost vertically. In generalized *Haplochromis* skulls (Fig. 5) and more particularly in skulls of elongate species, this part of the neurocranium lies parallel to a straight and gently sloping line connecting the foremost part of the ethmoid with the anterior extremity of the supra-occipital (Fig.

5, A). Posteriorly, the neurocranium does not differ significantly from the generalized type, except that the pharyngeal apophysis is not greatly depressed below the parasphenoid, and its pro-otic buttress is broad and bullate.

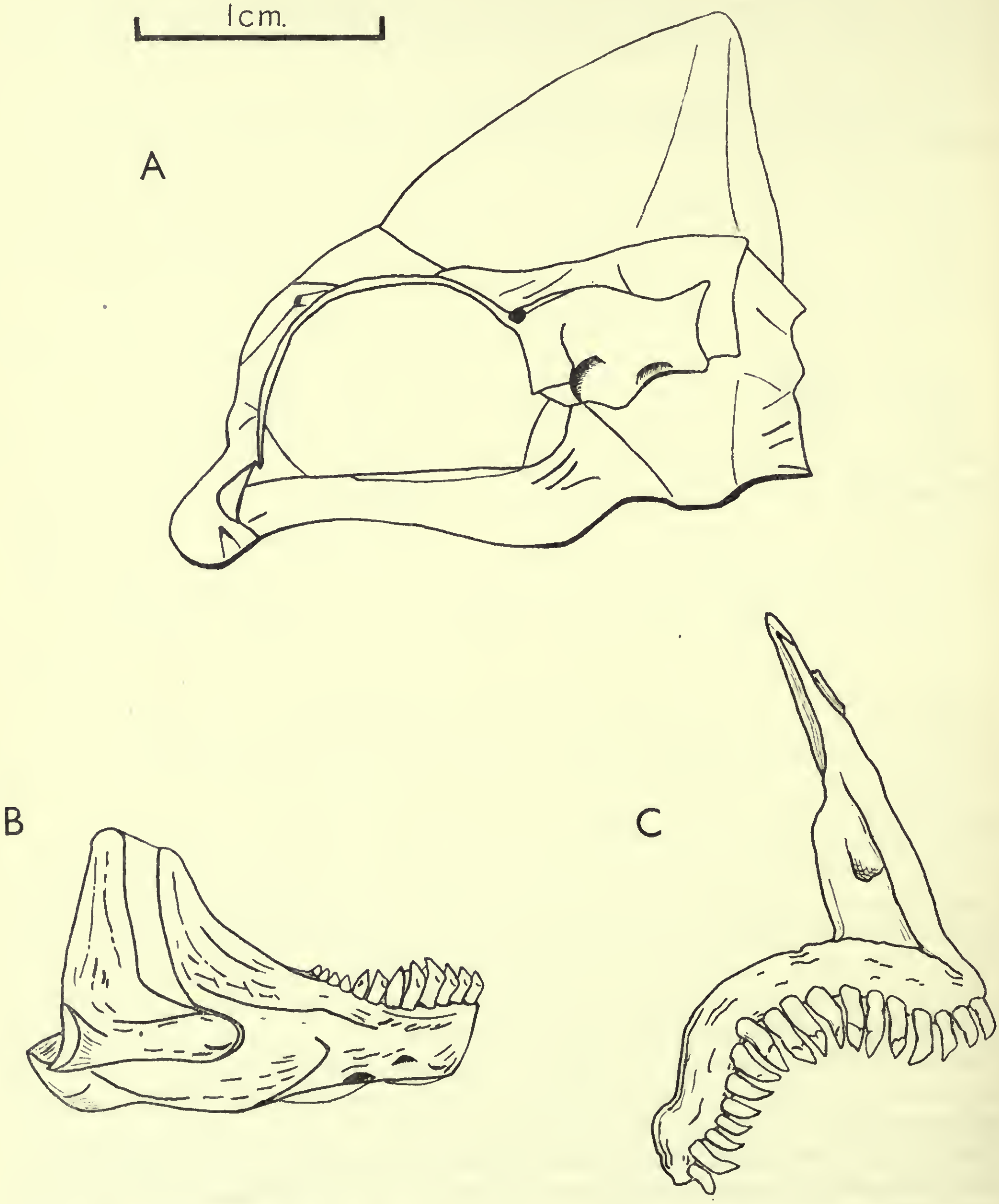


Fig. 4.—*Macropleurodus bicolor*. (A) Neurocranium in left lateral view; (B) dentary, (C) premaxilla, both in right lateral view. Skeleton prepared from a specimen of 115 mm. S.L.

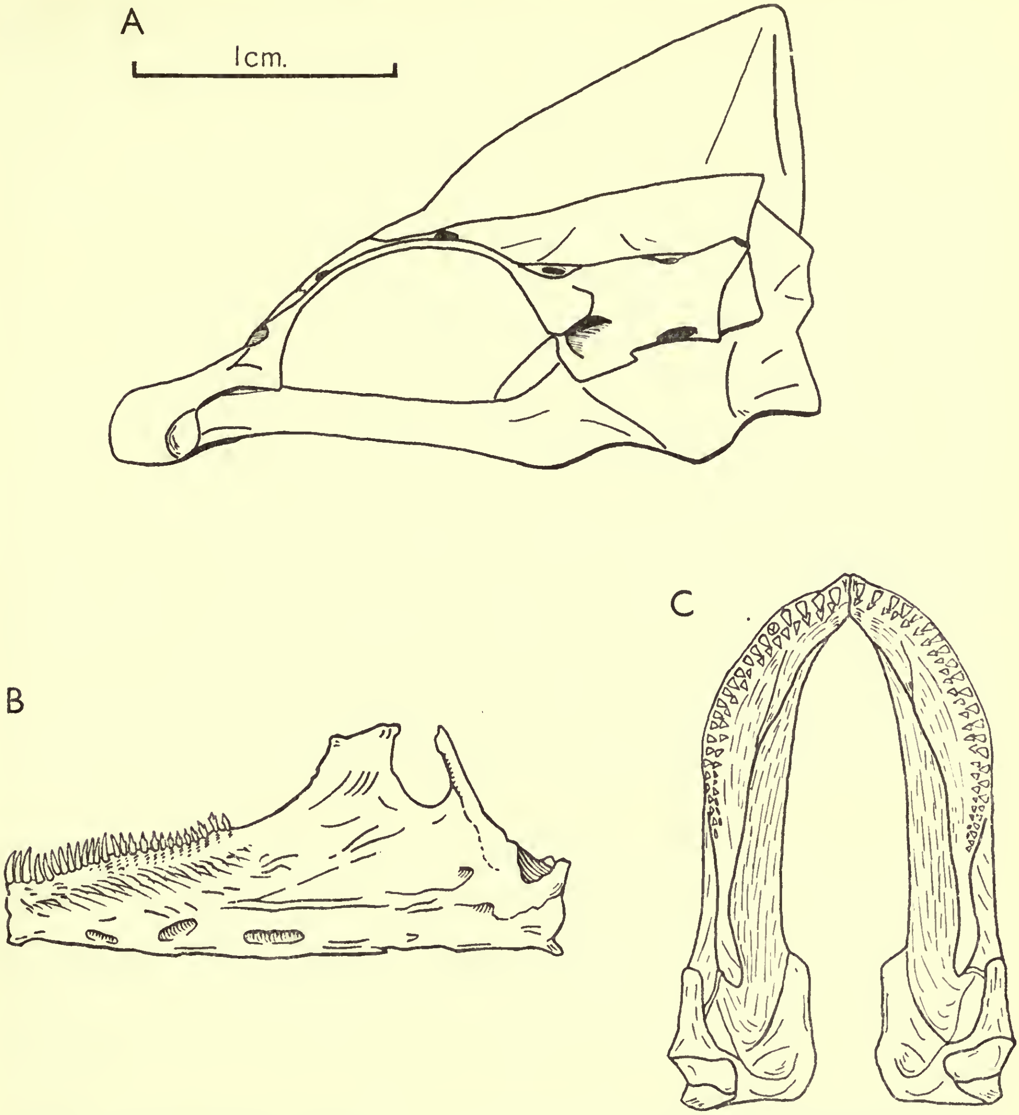


Fig. 5.—*Haplochromis michaeli.* (A) Neurocranium, (B) dentary, left lateral view ; (C) dentary, occlusal view ; to show the skull and jaws of a generalized *Haplochromis* from Lake Victoria. Skeleton prepared from a specimen of 115 mm. S.L.

The premaxilla shows considerable departure from the basic type found in most *Haplochromis* species. Whereas in *Haplochromis* there is slight ventral arching of the horizontal limb of this bone, in *Macropleurodus* the arch is greatly exaggerated, with its point of maximum curvature at the broadest part of the tooth band (Fig. 4, B). Individuals with a marked dextrally developed tooth pattern have a corresponding degree of asymmetry in the two halves of the premaxilla, which is then more acutely arched on the right side.

A comparative study of jaw musculature was made with *Haplochromis sauvagei* and *H. prodromus*, species in which the jaws show some deviation from the generalized *Haplochromis* condition towards that of *Macropleurodus*. Negligible differences were observed in the musculature of the three species, except that in *M. bicolor* the *adductor mandibulae* I measures only 28% of the head length, whilst in *H. sauvagei* and *H. prodromus* this muscle is 33% of head length. *Adductor mandibulae* II is also relatively shorter in *M. bicolor* (21·0% compared with 33·6% in *H. sauvagei* and 26·9% in *H. prodromus*). In all other respects the cranial musculature of *Macropleurodus* is typical for a generalized *Haplochromis* species.

Functional significance of the skull form, together with that of the well developed teeth, jaws and muscles, is best considered in relation to the predominantly molluscan diet of *M. bicolor*, and the manner in which its prey is secured. Whereas in most *Haplochromis* species the lower jaw is somewhat obliquely inclined when the mouth is shut, in *M. bicolor* it is almost horizontal. The position of the lower jaw at rest directly affects the manner in which the whole mouth is protruded; in typical *Haplochromis*, maximal protrusion is achieved as a result of the mandible moving from an inclined to a horizontal position. On the other hand, when the mouth of *M. bicolor* is opened, mandibular movement is from the horizontal to a point below it. Premaxillary movement is also directed downwards by the near vertical ethmoid complex over which the premaxilla slides. In consequence, the whole mouth is protruded ventrally, with the upper jaw slightly in advance of the lower. The short and broad *adductor mandibulae* muscles allow the mouth to be retracted with remarkable rapidity, thereafter mounting a powerful and sustained pressure on any object held between the teeth. The crushing power of the jaws is further enhanced by the stout outer teeth and well developed bands of lateral and postero-lateral inner teeth.

Aquarium observations show that *M. bicolor*, when feeding, usually approaches a snail from above, rapidly protruding the mouth in an attempt to snatch its prey from the substrate. Once the snail is firmly held and suitably orientated—generally with the foot directly orally—there follows a series of short biting movements which crush the shell and thus free the soft parts, which alone are ingested.

Attention has already been drawn to the similar skull structure in *M. bicolor* and *H. prodromus*; it is not surprising therefore to find that both species have similar feeding habits.

Ontogeny. Alizarin preparations of larval *M. bicolor*, *H. macrops* (a generalized species), and *H. prodromus* have been compared. These specimens reveal no fundamental differences in osteology or dentition of the three species when compared at morphologically equivalent developmental stages. For example, at the latest stage examined (9·0 mm. total length; yolk sac almost completely resorbed) the small conical outer teeth are morphologically and numerically identical in all three species.

From these admittedly few observations it would seem that characteristic adult skull form and outer teeth must develop during post-larval ontogeny.

Coloration and polychromatism

Coloration in life. Adult females with greenish-yellow ground colour, becoming lighter or silver ventrally. Dorsal and anal fins yellow-green, the former with or without two irregular, dark, longitudinal stripes, the latter with two to four ill-defined yellow spots on the posterior part. Caudal and ventral fins generally colourless, though the latter may sometimes be slightly dusky. Young of both sexes and sexually inactive males have similar coloration.

Adult males (breeding coloration). Dark slate-blue ground colour, lighter, sometimes silver, ventrally. Chest, branchiostegal membrane, lower jaw and ventral aspects of the cheek, black. Operculum and flank sometimes with a faint scarlet flush. Dorsal fin dusky, with deep red spots and streaks between the rays, especially intense on the soft part. Anal dusky, with well marked scarlet ocelli. Ventral fins black. Intensity of male coloration is correlated with sexual state ; inter-grades are known between the coloration described above and that of typical female or juvenile coloration.

Besides normal sexually dimorphic coloration, certain fish exhibit a third colour pattern, in the form of an individually variable piebald, black on a yellow-green ground. The holotype is such a specimen (Fig. 1). The *bicolor* pattern is clearly composed of vertically arranged irregular and often interrupted dark bands, which are generally continued across the body on to the vertical and paired fins. Although some are more intensely blotched than others, no intergrades are known between normal female coloration and *bicolor* variants.

With two exceptions all *bicolor* individuals examined were females. The colour-pattern and degree of pigmentation differ in the two exceptional male fishes. Since protandry might be suspected, the gonads were sectioned and examined microscopically. In both fishes, however, there was evidence only of testicular tissue. In one fish the pattern is typical ; in the other the pattern is less intense and occurs on a darker ground than is typical for female fishes.

Accurate frequency-estimates for *bicolor* individuals are difficult to obtain, since collectors show marked sampling bias in favour of these strikingly coloured fishes. However, in more rigorously controlled collections from one area, *bicolor* frequency amongst female fish in the 105 mm. to 125 mm. size class is approximately 30%, an incidence sufficiently high to justify regarding the phenomenon as being due to polymorphism and not to the maintenance of an atypical phenotype by recurrent mutation.

If the two female colour patterns are accepted as an example of polymorphism, it is necessary, *ex hypothesi*, to consider the selective balance which must exist between the two forms. This question is further complicated by the apparently almost completely sex-limited polymorphism in *M. bicolor*.

Since the genetical basis of polymorphism and sex determination is unknown for *Macropleurodus*, some hypothesis at least is desirable before considering the question of selective values for the two colour patterns.

If, as in many fishes, the female is the heterogametic sex, then a possible (and doubtless oversimplified) explanation for this sex-limited polymorphism is that the gene or gene complex underlying development of a *bicolor* pattern may lie in a sex chromosome, be recessive to the gene or genes for normal colour, and be linked with a recessive lethal gene. Thus full expression of *bicolor* pattern could only be manifest in the heterogametic sex. Males carrying the double complement of recessive *bicolor* genes necessary for phenotypic expression in that sex, would, on the linkage supposition, die as a result of simultaneously receiving the two recessive lethal genes. Since linkage is sometimes broken, a small percentage of male *bicolor* individuals might well be expected and the two *bicolor* male fishes in this collection are possibly such individuals.

By this reasoning, either selection in favour of polymorph genes must be sufficient to compensate for loss of males and consequent unbalance of the sex-ratio or, alternatively, the unbalanced sex ratio may be the factor preventing spread of *bicolor* genes throughout the species, should these have a selective value slightly higher than " normal ".

Two possible advantages associated with *bicolor* patterns, or genotypes, present themselves. Firstly, a *bicolor* pattern is, in effect, a disruptive one and may thus provide some protection against the attacks of predators. Studies on fish-eating birds (Cott, 1952) and on piscivorous fishes such as *Bagrus* and *Clarias* (personal observation) neither support nor negate this possibility, since *M. bicolor* has not been found among the prey of these animals. Secondly, there is the possibility, also unproven, that a female *bicolor* genotype, or a male heterozygous for *bicolor*, may possess some physiological advantage over other genotypes.

Regrettably, then, insufficient positive evidence is available at present to warrant further discussion on the evolutionary aspects of polymorphism in *Macropleurodus*.

Ecology

Habitat. M. bicolor is widely distributed within Lake Victoria, occurring most frequently in littoral and sublittoral regions, especially where the bottom is hard (sand, rock or shingle), but only rarely over mud. Depth distribution is fairly restricted, with a maximum of between 30 and 40 feet (see also Graham, 1929).

Food. From gut analyses of numerous specimens (throughout the size range 60–150 mm.) it is apparent that snails and insect larvae are the predominant food organisms (see also Graham, 1929). Shell fragments are rarely found in the stomach or intestine although opercula are usually present. Aquarium observations confirm that almost the entire body of the snail is removed from its shell before ingestion takes place (*vide* p. 325), although small snails and, on occasion, thin-shelled species, may be crushed intra-orally before being swallowed. As a result of this feeding mechanism snail remains are so fragmentary as to preclude accurate identification ; remains of *Gabbia* sp. have, however, been positively identified on several occasions.

The insects most commonly recorded from the pabulum of *M. bicolor* are larvae of the boring may-fly, *Povilla adusta* Navás, with other larval Ephemeroptera, and larval Chironomidae occurring less frequently. The proportion of insect to molluscan food eaten is difficult to determine and is probably related to local and cyclic abundance of these organisms.

In the light of numerous gut analyses which are now available for this species, Graham's record (1929) of fish and cichlid eggs from the stomach of *M. bicolor* requires some comment. Apart from this record no other instances of piscivorous habits are known for *M. bicolor*. Unfortunately, Graham does not give a detailed analysis of the gut contents, particularly of the number of specimens from which his data are derived. Bearing in mind this limitation, it is suggested that the fish-remains and eggs were from the stomachs of different individuals and consequent upon brooding female fishes swallowing their own young, a relatively common occurrence when the fishes are caught in gill-nets.

Breeding. The exact spawning grounds of *M. bicolor* are unknown : eggs and larvae at all stages of development have been found in the mouths of various female fishes and it is presumed that the species is a mouth-brooder. Brooding females have been caught in all parts of the species range. The smallest sexually active fish examined was a female 96 mm. long (*ex* Kisumu). The habitat of post-larval fishes is unknown.

Affinities

Unlike the other monotypic genera *M. bicolor* can apparently be related to an extant species of *Haplochromis*. Similarity in skull architecture of *M. bicolor* and *H. prodromus* has already been noted. There are additional similarities in the short and stoutly constructed jaws of both species, besides a marked resemblance in general facies. Against these resemblances must be set the very different tooth form and dental pattern of *H. prodromus*, although in this species the teeth are stout and the inner series well developed. The structure of the head and dental patterns suggest that, at a functional level, the condition represented by *H. prodromus* might well be considered pre-adaptive to the development of a relatively massive dentition, such as that of *M. bicolor*.

Study material and distribution records

Museum and Reg. No.	S.L. (mm.).	Locality.	Collector.
British Museum (N.H.) :			
1906.5.30.414 (type of *H. bicolor*)	125	Bunjako (Uganda)	Degen
1906.5.30.378	115	Ditto	„
1928.5.24.493–503	115–125	See below	M. Graham
1928.5.24.1–3	120–125	Ditto	Ditto
Paris Museum :			
12.278 (holotype of *H. materfamilias*	109	Port Florence, Kenya	Alluaud and Jeannel
12.279–281 (paratypes of *H. materfamilias*; proportions not included in description above)	91–97	Ditto	Ditto
Genoa Museum :			
(Type of *Bayonia xenodonta* Blgr.)	73	Jinja	Bayon
B.M.(N.H.) :			
1955.2.10.5–11	78–110	Kisumu	E.A.F.R.O.
1955.2.10.50–57	101–123	Jinja, Napoleon Gulf	Ditto
1955.2.10.43–46	79–104	Beach nr. Nasu Point, Buvuma Channel	„

Museum and Reg. No.	S.L. (mm.).	Locality.	Collector.
B.M.(N.H.):—*cont.*			
1955.2.10.22–23	82 and 97	Grant Bay (Uganda)	E.A.F.R.O.
1955.2.10.21	102	Dagusi Island	Ditto
1955.2.10.65–73	105–120	Off southern tip of Buvuma Is.	,,
1955.2.10.24–42 and 74–83	90–122	Harbour at Entebbe	,,
1955.2.10.58–62	58–67	Bugonga Beach	,,
1955.2.10.12, 16–20 and 48	112–130	Busongwe Bay (Kagera River mouth)	,,
1955.2.10.63–64	110 and 147	Majita Beach (Tanganyika Terr.)	,,
1955.2.10.4, 49 and 84	115–119	Mwanza	,,

Graham (1929) records the occurrence of *M. bicolor* as follows:

Kenya: Kavirondo Gulf: Off Sukuri Island.
Off Ulambwi bay.
Mbita Passage.
Near Nzoia River.
Kadimu Bay.
Tanganyika Territory: Mwanza.
Smith Sound.

Genus ***PLATYTAENIODUS*** Boulenger, 1906

Platytaeniodus Boulenger, 1906, Ann. Mag. nat. Hist. (7) **17**, 451; *Idem*, 1907, Fish. Nile, 493; *Idem*, 1915, Cat. Afr. Fish. **3**, 426, fig. 292; Regan, 1922, Proc. zool. Soc., Lond. 190. Type species: *Platytaeniodus degeni* Blgr. 1906.

Generic synonyms:

Astatotilapia (part) }
Haplochromis (part) } For references see synonymy under species.

Generic characters and synonomy

Both Boulenger and Regan considered the premaxilla and its tooth pattern diagnostic. Boulenger (1914) states:

" . . . the alveolar surface of the premaxilla widening towards the pharynx, the band of teeth in the upper jaw horseshoe shaped . . . "

Additional material shows, however that in fishes below 100 mm. standard length the posterior premaxillary dentigerous (alveolar) surfaces are not always expanded medially. Nevertheless, even in small specimens the premaxilla is stouter and its dentigerous surface wider than in *Haplochromis*; posteriorly the teeth are arranged in several rows, so that the premaxillary tooth band is always clearly U-shaped, with the arms at least as broad as the medial part. Broadening of the posterior alveolar surfaces is gradual and shows positive allometry with standard length; in some large individuals the left and right surfaces are closely apposed in the mid-line (Fig. 6, c).

Tooth bands in the lower jaw are more readily diagnostic and less subject to variation with absolute size than those of the premaxilla. In *Platytaeniodus* the mandibular teeth are confined to the anterior and antero-lateral portions of the dentary and are grouped into two broad and roughly pyriform patches, contiguous at the symphysis; posteriorly there is a short, single row of four to seven teeth

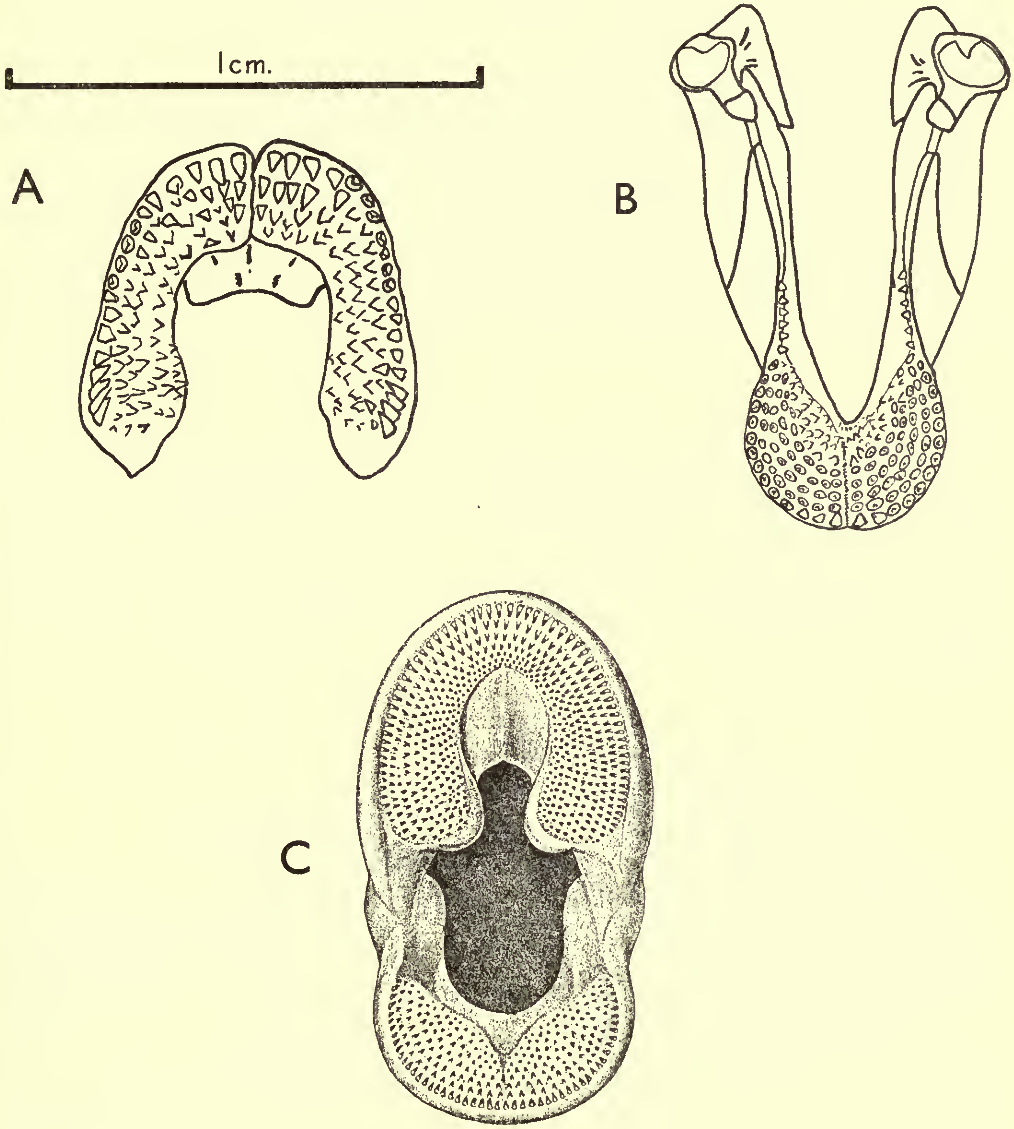


Fig. 6.—*Platytaeniodus degeni.* (A) Premaxilla, (B) dentary, both in occlusal view. Skeleton prepared from a specimen 80 mm. S.L. (C) Mouth of the holotype, *ca.* × 4. [(C) from Boulenger, *Fishes of the Nile.*]

lying between the ascending part of the ramus and the anterior tooth bands (Fig. 6, B and C).

When provisionally referring *Astatotilapia jeanneli* Pellegrin to *Haplochromis macrops* Blgr., Regan (1922) was apparently misled by the large eye and shallow preorbital of *A. jeanneli*. There is undoubtedly some resemblance between *H. macrops* and *P. degeni*, but this is confined to superficial characters, and is belied by their fundamentally different dentition. Re-examination of the types of *A. jeanneli* reveals that the premaxillary teeth are arranged in four or five series of equal breadth both laterally and posteriorly, a condition never observed in *H. macrops*. Furthermore *A. jeanneli* has the mandibular teeth grouped anteriorly and laterally in five series, with only a short, single series posteriorly. That is to say, both type specimens have a dentition typical for small *P. degeni*. In other characters too, notably the mouth with its broad lower jaw, shorter than the upper, and the almost completely hidden maxilla, *A. jeanneli* agrees more closely with *P. degeni* than does *H. macrops* or any other *Haplochromis* species.

On these grounds, therefore, I consider *A. jeanneli* to be synonomous with *P. degeni*.

Diagnosis

Cichlid fishes of the *Haplochromis* group, but differing from *Haplochromis* in having broad bands of teeth on the posterior part of the premaxillary dentigerous surface, which is expanded medially in large specimens but is of almost equal breadth anteriorly and laterally in fishes of less than 100 mm. S.L. Teeth on the dentary grouped into two, broad, pyriform, curved and contiguous bands anteriorly and antero-laterally, but continued posteriorly as a short single row only. Lower jaw usually shorter than the upper; maxilla almost completely hidden below the preorbital.

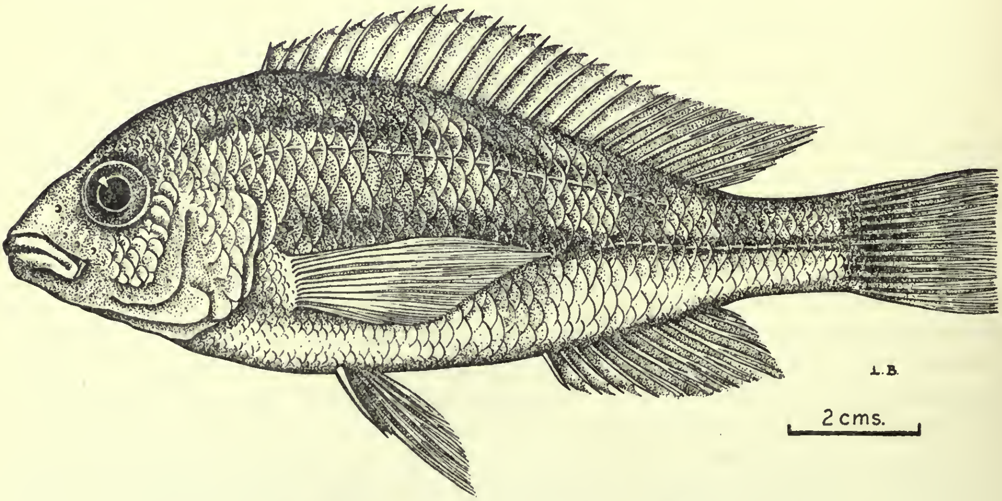


FIG. 7.—*Platytaeniodus degeni*, ♀. Drawn by Miss L. Buswell.

Platytaeniodus degeni Boulenger, 1906

(Fig. 7)

Platytaeniodus degeni Boulenger, 1906, *l.c.*; 1907, *l.c.* and pl. xci, fig. 1; 1915, *l.c.* and fig. 292; Regan, 1922, 190, fig. 14.
Astatotilapia jeanneli Pellegrin, 1913, Bull. Soc. zool. France, **37**, 313.
Haplochromis jeannelli (Pellegrin), Blgr. 1915, Cat. Afr. Fish. **3**, 291.
Haplochromis macrops (part) Regan, 1922, Proc. zool. Soc. London, 166.

Description

Thirty-six specimens (size range 67 to 154 mm.) comprising the type and other specimens in the British Museum (Nat. Hist.) (including material newly collected by E.A.F.R.O.), as well as the types of *A. jeanneli* are considered in this description.

Since most characters tabulated below show some allometry with standard length these data are grouped into two size classes. In some characters intra-group variability is high, but further subdivision into smaller groups is impracticable.

In the table of proportions, head length, depth of body and length of caudal peduncle are expressed as percentages of standard length; all other characters are expressed as percentages of head length. Range and mean are given for each character.

Table I.

Standard Length.	67–93 mm. (23 specimens).	98–154 mm. (13 specimens).
Depth of body	32·5–40·5 M = 35·6	34·78–43·0 M = 38·4
Length of head	30·0–36·5 M = 32·4	31·5–34·7 M = 32·7
Depth of preorbital	12·0–16·0 M = 14·2	13·7–17·4 M = 15·2
Least interorbital width	25·0–30·8 M = 27·1	28·2–34·8 M = 31·2
Length of snout	25·0–32·0 M = 30·0	31·75–37·4 M = 34·8
Diameter of eye	27·4–33·4 M = 30·8	22·1–26·0 M = 24·8
Depth of cheek	18·5–26·1 M = 19·7	20·0–26·6 M = 23·4
Length of lower jaw	32·1–39·6 M = 37·0	35·0–38·1 M = 36·0
Caudal peduncle	13·9–21·5 M = 16·5	14·0–18·5 M = 16·7

Dorsal profile of head and snout gently (in a single specimen somewhat strongly) decurved; mouth horizontal; lower jaw equal to or more usually shorter than upper, its length/breadth ratio 1·16–1·68: in some specimens the lower jaw, including lips, is slightly broader than the upper. Lips well developed and somewhat thickened; maxilla almost completely hidden beneath the preorbital, with only its postero-ventral tip exposed and extending to below the anterior orbital margin, or slightly beyond.

The holotype, a male of 115·0 mm. S.L., is figured by Boulenger (1907 and 1915). This fish is both somewhat atypical and slightly distorted in preservation and the impression given of a deep ventral profile and a slightly oblique mouth is not characteristic.

Gill rakers. Short and stout, 7–8 on lower limb of the anterior arch, the lowest one or two usually reduced.

Dentition. Premaxilla with 4–8 rows of teeth ; dentary with 4–6 rows.

With few exceptions, specimens over 100 mm. S.L. have the posterior part of the premaxillary dentigerous surface expanded medially, so that the upper tooth bands are broader posteriorly than anteriorly. In small individuals, although there are several series of teeth posteriorly, the tooth band is either of equal width at all points, or medial expansion of the premaxilla may have begun, causing the band to be very slightly wider posteriorly (Fig. 6, A). Expansion of the posterior surface is not correlated with an increase in the number of tooth rows borne on it, which are, in fact, equal to or slightly fewer than those on the anterior part of the premaxilla.

Mandibular dental pattern as described for the genus ; pyriform band from half to two thirds as broad as long.

Teeth are variable in form, those of the outer series slenderly conical, with or without an admixture of unequally bicuspid teeth. Teeth of the inner series all unicuspid in most specimens above 100 mm. S.L. and in some below that size ; otherwise the outermost teeth unicuspid and the remainder tricuspid or exceptionally, bicuspid.

Scales ctenoid ; lateral line interrupted, with 31 (f.2), 32 (f.5), 33 (f.14), 34 (f.10), 35 (f.2), or 36 (f.3) scales. Cheek with 3–4 series of imbricating scales ; 7–9 scales between lateral line and origin of dorsal fin ; 7–9 (rarely 10) between the pectoral and pelvic fins.

Fins. Dorsal with 24 (f.3), 25 (f.23) or 26 (f.10) rays, anal with 11 (f.6), 12 (f.23) or 13 (f.7) rays, comprising XV–XVII 8–10 and III 8–10 spinous and soft rays. Pectoral fin 22·6–31·8 (M = 28·0) per cent of standard length. Caudal truncate, scaled on its proximal half only. Pelvics with the first ray produced, extending to the vent in a few specimens and to the spinous part of the anal in most.

Syncranium. Since the form of premaxilla and dentary in *P. degeni* is correlated with the well-developed tooth pattern, both these bones depart very strikingly from the typical *Haplochromis* condition.

In small individuals of *P. degeni*, the premaxilla bears a superficial resemblance to that of *Hoplotilapia*, particularly with regard to the dental pattern, but in large fishes it is unique. On the other hand, the dental pattern and morphology of the dentary are comparable in both large and small individuals. The dentary is characterized by its broad and laterally expanded anterior tooth-bearing portion, which imparts to this bone an appearance unique amongst the Lake Victoria cichlids.

The neurocranium of *P. degeni* is intermediate between the generalized *Haplochromis* type and that of *M. bicolor*. It is strictly comparable with the neurocrania of species of the *H. crassilabris* group. Here the skull is characterized by a somewhat shortened and steeply inclined ethmo-vomer complex ; in consequence, the anterior skull profile is also steep. In a typical *Haplochromis* skull the ethmo-vomer is longer and rises less steeply, meeting the downward sloping frontals at a wide angle. As a result, the anterior profile is shallower and also more acute than in the " *crassilabris* " type skull (Fig. 5).

Jaw musculature in *P. degeni* dos not differ greatly from that of a generalized *Haplochromis* species.

Coloration. Preserved material. Males : dusky to dark grey ; dorsal and anal fins dark ; pelvics black, caudal colourless. *Females and immature individuals :* silver-grey or light brown ; fins colourless.

Transverse and longitudinal banding sometimes occurs, being most clearly marked in females and young individuals ; when present, there is a well marked median longitudinal stripe, a fainter and interrupted band running slightly below the dorsal fin, and eight or nine narrow transverse stripes on the flank and caudal peduncle. Faint lachrymal and interocular stripes may also be present. The presence and intensity of these markings is apparently related to the emotional state of the fish or may only appear after death.

Coloration in life. Sexually active males : ground colour light blue-grey, lips iridescent blue. Chest and branchiostegal membrane black. Fins ; dorsal sooty, lappets and spots on soft part red ; caudal with red flush, most intense along margin ; anal with dusky pink flush and several yellow ocelli. *Females :* ground colour golden fawn ; all fins neutral, dorsal with orange lappets and spots, especially on the soft part ; caudal with orange margin and maculae ; anal with faint or well marked yellow ocelli.

Ecology

P. degeni is recorded from several areas in Lake Victoria (see below), but as so few specimens are known it is not possible to generalize on habitat preferences. From the scanty data available it appears that the species is probably restricted to littoral and sub-littoral regions where the water is less than fifty feet deep. Specimens have been caught in nets set over both hard and soft substrates, but the greater number came from stations having a sand or shingle bottom.

Food. The distinctive dentition of this species suggests a highly specialized diet. Tantalizingly few fish, however, have yielded ingested material. Twelve specimens have been examined, all of which were caught in nets set overnight or in seines operated during varied daylight hours. According to the substrate over which they were living, ten fishes had either sand grains or organic mud in the stomach and intestines, together with fairly dense aggregations of mucus. Two fishes, caught on different occasions at a station near the southern tip of Ramafuta Island (Buvuma Channel), had the entire alimentary tract filled with the diatom *Melosira.* Diatoms from the stomachs of these fishes showed only slight signs of digestion, but samples taken from the mid-intestines and recta were almost completely digested. Animal remains, occurring sporadically, included insect larvae, Hydracarina, fragments of Copepoda, Ostracoda, and in two specimens shell fragments of Pelecypoda (Sphaeriidae).

Most guts also contained some diatoms and blue-green algae, the former apparently digested, the latter intact. The very small quantity of ingested material in any one individual is striking and no particular organism, or group of organisms, occurs with sufficient frequency to indicate what the food of *P. degeni* may be. Since sand and bottom debris is significant in the majority of specimens, it is possible that the species may feed on the micro-fauna and flora living on and within the substrate. Thus, broad bands of jaw teeth may serve to rasp and loosen food from the surrounding sand.

Breeding. Spawning sites are unknown ; only two females, both from beaches in the Mwanza area, have been found with eggs in the mouth. The smallest individual with demonstrably active gonads was a female, 71·0 mm. long.

Affinities

There is no obvious relationship between *P. degeni* and any known Lake Victoria species or species-group of *Haplochromis*, with which genus the species shows fundamental affinities. The peculiar premaxillary and mandibular tooth patterns serve to set *P. degeni* apart from even those *Haplochromis* with several series of inner teeth. Regan (1922) considered *P. degeni* as being " very near " to *H. prodromus*, which species he believed " shows a slight departure from the normal *Haplochromis* dentition towards the *Platytaeniodus* type ". His opinion was based on the holotype and then unique specimen of *H. prodromus*. Summarizing unpublished data on *H. prodromus*, it is clear that the type specimen has an aberrant dental pattern and that its resemblance to *P. degeni* is purely superficial. Whereas in large *Platytaeniodus* there is an actual expansion of tooth-bearing surfaces, in *H. prodromus* only the tooth-band is apparently expanded ; its increased breadth is actually due to the posterior teeth being more widely separated from one another than are the anterior teeth. In no specimen of *H. prodromus* is the upper tooth band as broad posteriorly as anteriorly, yet this is the usual condition in *P. degeni*. Further, the dentary of *P. degeni* differs considerably from that of *H. prodromus*. The evolution of a wholly multi-seriate dentition has probably occurred more than once within the Lake Victoria species-flock, as for instance in the *H. sauvagei* group and again in the monotypic genera. Thus any apparent relationship between *P. degeni* and *H. prodromus* should be considered as consequent upon convergent evolutionary trends, the ultimate expressions of which are achieved by manifestly dissimilar means.

Study material and distribution records

Museum and Reg. No.	S.L. (mm.).	Locality.	Collector.
British Museum (Nat. Hist.) :			
1906.5.30.511 (holotype)	114	Bunjako (Uganda)	Degen
1909.3.29.10	98	Sesse Is. (Uganda)	
1928.5.24	93	Mbita Passage (Kenya)	M. Graham
Paris Museum :			
12.262 (holotype of *A. jeanneli*)	72	Port Florence (Kenya)	Alluaud and Jeannel
12.262 (paratype of *A. jeanneli*)	67	Ditto	Ditto

Museum and Reg. No.	S.L. (mm.).	Locality.	Collector.
B.M. (N.H.) :			
1955.2.10.91–94	73–79	Kisumu (Kenya)	E.A.F.R.O.
1955.2.10.105–106	78–90	Kamarenga (Kenya)	Ditto
1955.2.10.115	74	Kendu (Kenya)	„
1955.2.10.88	74	Likungu (Kenya)	„

Genus **HOPLOTILAPIA** Hilgendorf, 1888

Hoplotilapia Hilgendorf, 1888, S.B. Ges. naturf. Fr. Berlin, 76–77 (type species (*Paratilapia* ?) *retrodens* Hilgendorf, l.c.) ; Regan, 1922, Proc. zool. Soc., Lond. 190.

Cnestrostoma Regan, 1920, Ann. Mag. nat. Hist. (9) **5**, footnote p. 45 (type species *Paratilapia polyodon*, Blgr.).

Haplochromis (part) }
Paratilapia (part) } For references see synonymy under species below.
Hemichromis (part) }

Generic characters and synonymy

The holotype of *Hoplotilapia retrodens* (in the collections of the Zoologisches Museum der Humboldt-Universität, Berlin) has not been examined by me, nor can it be definitely established whether this specimen is still in existence. Dr. Kurt Deckert of the Zoologisches Museum has, on two occasions, kindly attempted to locate several specimens, including the type of *H. retrodens.* Of these he writes : " Ich muss Ihnen leider mittheilen, dass unser Suchen nach den verlangten Typen ohne Erfolg geblieben ist, obwohl ich mit grosser Sicherheit anneheme, dass sie nicht verloren-gegangen sind."

Hilgendorf's original description of (*Paratilapia?*) *retrodens* (1888), although brief and lacking detail, nevertheless stresses characters which clearly separate this species from others of the *Haplochromis* group : viz. a multi-seriate dental pattern with stout and enlarged posterior teeth. Pfeffer's redescription (1896) of the same specimen confirms and extends this account. In the material at my disposal, however, the posterior teeth are clearly enlarged only in the upper jaw, and not in both, as stated for the type. Specimens described below agree closely with the type in the other characters described by Hilgendorf and Pfeffer ; slight differences in scale numbers can probably be attributed to different methods of making these counts.

In addition to the four specimens of *H. retrodens* in the British Museum (Nat. Hist.) it has been possible, through the kindness of Dr. Delfa Guiglia, to examine the type of *Paratilapia polyodon* Blgr. and one other specimen (Museo Civico di Storia Naturale, Genoa, reg. no. G.E. 12.994) determined by Boulenger as *P. polyodon*, and to confirm Regan's view (1922) that these are conspecific with *H. retrodens.*

Diagnosis

Differing from *Haplochromis* as defined by Regan (1920 and 1922*b*) in having broad bands of teeth in both jaws, well developed and usually of almost uniform breadth throughout or very slightly narrower posteriorly. Posterior teeth of the upper jaw enlarged and stout, those of the lower jaw slightly, if at all, enlarged, but the tooth-band continued posteriorly on to the steep ascending contour of the dentary. Lower jaw wide and flat, almost square in anterior outline, slightly shorter than the upper.

Since only three of the collected specimens of this genus are small it is not possible to generalize on differences which apparently exist between the dentition of adult

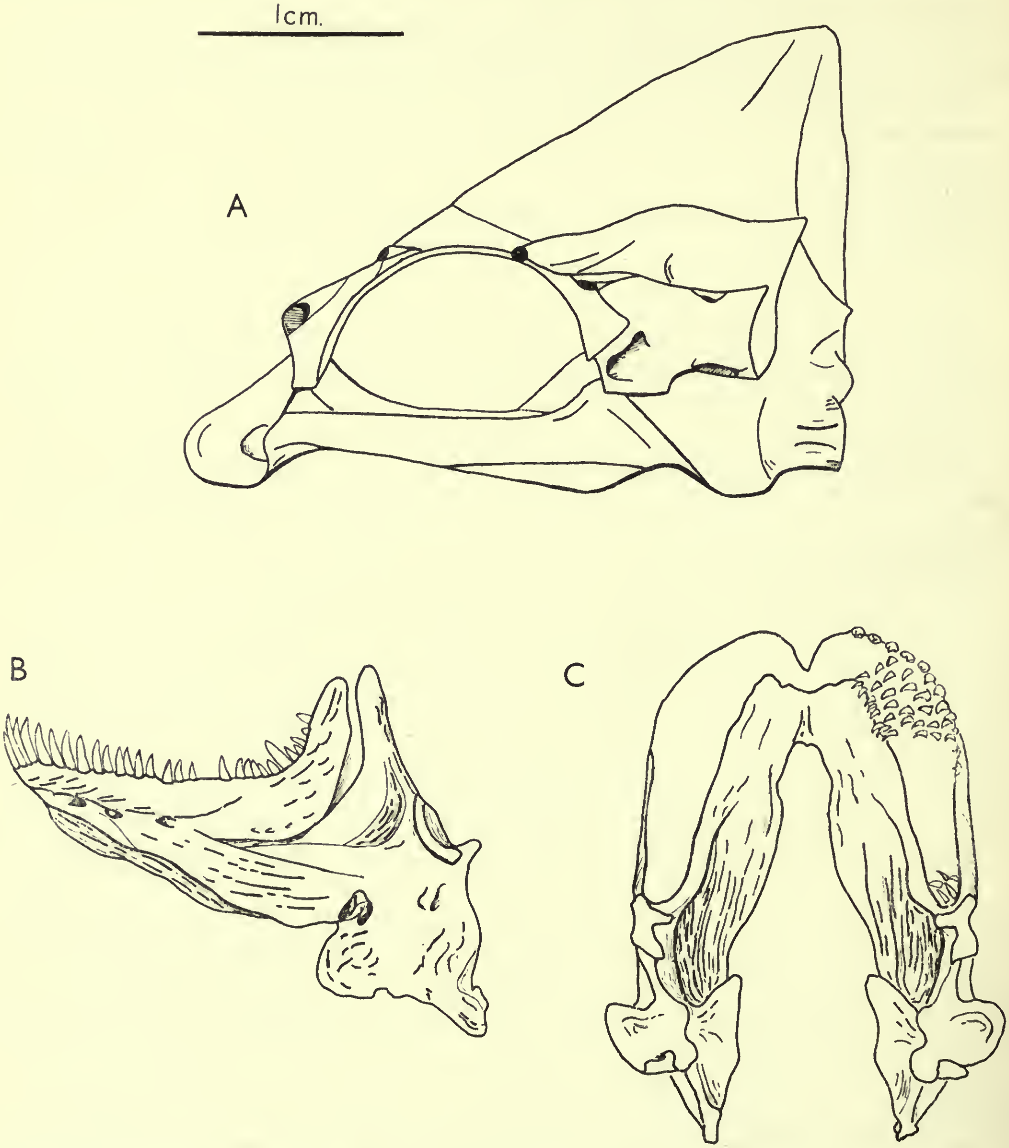


FIG. 8.—*Hoplotilapia retrodens*. (A) Neurocranium, (B) dentary in lateral view, (C) dentary, occlusal view. Dentition only part indicated. From a specimen of 125 mm. S.L.

and juvenile fishes. In these three specimens (74·0, 76·0 and 55·0 mm. S.L.) the tooth bands are broad anteriorly, being composed of 5, 3, and 3 series respectively. Laterally, however, they are reduced to two series, whilst postero-laterally only the outer series persists. In none is the dentition continued onto the ascending part of the dentary, although the shape of the lower jaw is as in the adult.

Two adults of 96 and 110 mm. S.L., collected in a single seine haul at Bukakata, retain these presumedly juvenile dental characters. They form a graded morphological series with a third specimen (134·0 mm. S.L., from the same station) which exhibits only slight departure from the " typical " condition.

The broad and shallow lower jaw (Fig. 8, B and C) of typical individuals is unique amongst Lake Victoria Cichlidae. A few specimens of *H. retrodens* have the dentary, at least in external appearance, similar to that of *Haplochromis*, although in every case the dental pattern is typical for *Hoplotilapia*.

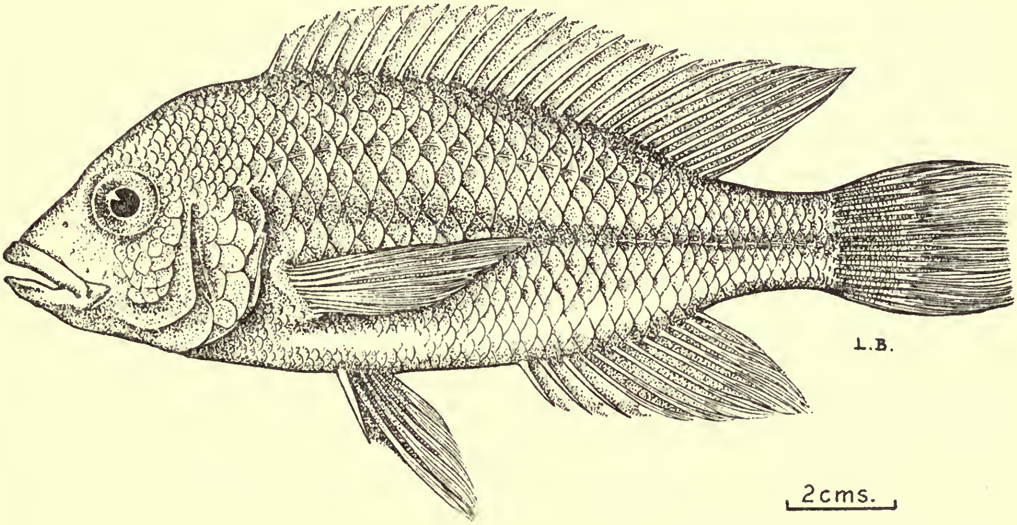


FIG. 9.—*Hoplotilapia retrodens*, ♀. Drawn by Miss L. Buswell.

Hoplotilapia retrodens Hilgendorf, 1888

FIG. 9.

(*Paratilapia* ?) *retrodens* Hilgendorf, 1888, S.B. Ges. naturf. Fr. Berlin, 76.
Hoplotilapia retrodens Hilgendorf, t.c., 77.
Hemichromis retrodens, Pfeffer, 1896, Thierw. O. Afr. Fische, 19.
Haplochromis bicolor (part) Boulenger, 1906, Ann. Mag. nat. Hist. (7) **17**, 444 ; two specimens B.M. no. 1906.5.30.417 and 418.
Paratilapia bicolor (part) Boulenger 1915, Cat. Afr. Fish. **3**, 346.
Paratilapia polyodon Boulenger, 1909, Ann. Mus. Genova (3) **4**, 306, fig. ; *Idem*, 1911, *ibid.* **5**, 68 ; *Idem* 1915, Cat. Afr. Fish. **3**, 349, fig. 236.
Cnestrostoma polyodon (Boulenger), Regan, 1920, Ann. Mag. nat. Hist. (9) **5**, footnote p. 45.

Description

From available material it would appear that only the interorbital width shows marked allometry with standard length. It must, however, be borne in mind that paucity of specimens within the smaller and larger size groups may obscure such relationships, especialy since, in those size-groups which are well represented, individual variability is high. With the exception therefore of interorbital width, ranges and means are given for the sample as a whole. For interorbital width the range and mean are given for three size groups, 74–115 mm. (N = 21), 116–130 mm. (N = 32), and 131–144 mm. (N = 11).

Depth of body 31·6–41·6 (M = 38·3), length of head 30·1–34·8 (M = 32·0) per cent of standard length. Dorsal profile of head and snout straight or slightly concave, steeply sloping. Preorbital depth 12·5–18·8 (M = 16·4) per cent of head length; least width of interorbital 24·2–33·8 (M = 28·7), 28·6–35·1 (M = 31·5) and 31·1–33·4 (M = 31·6) per cent for the three size groups respectively; length of snout 29·0–36·8 (M = 32·5), eye 23·8–29·6 (M = 26·9), depth of cheek 19·5–28·2 (M = 23·9) per cent of head length.

Lower jaw slightly shorter than upper 33·7–40·8 (M = 38·2) per cent of head, the length/breadth ratio from broader than long to 1·33 times as long as broad. Mouth horizontal, lips somewhat thickened. Posterior tip of the maxilla extending to the vertical from the anterior margin of the orbit or as far as the pupil.

Described from 64 specimens, 55–144 mm. standard length.

With few exceptions, there is remarkable uniformity in the general facies of *H. retrodens*. In this respect the figure of *Paratilapia polyodon* type specimen in Boulenger (1909 and 1915) can be considered fairly representative. The lower jaw in this specimen has, however, been broken and subsequently distorted in preservation, consequently the ventral head profile of the figured specimen is inclined upward and is not horizontal, as it would be in life. The greatest departure from typical physiognomy and body form is seen in a single specimen from Bukoba (Tanganyika) which has the body relatively elongate and the head profile strongly curved. Despite this aberrance in gross morphology, the dentition and other fundamental characters of this specimen are typical.

Teeth and dental pattern. Fishes above 90 mm. S.L. have 5 to 8 series of teeth anteriorly and 4 to 5 series posteriorly in the upper jaw; 5 to 8 (rarely 9 or 10) series anteriorly and 3 to 5 series posteriorly in the lower jaw. From 40 to 68 teeth in outer series of the upper jaw. Teeth small, those of the outermost series largest, variable in form, but usually unicuspid; some bi- and tricuspid teeth occur in the inner series. Two specimens from Majita and Mwanza (Tanganyika Territory) have markedly aberrant, stoutly conical or nearly molariform teeth in all series of both jaws. In both specimens the dental pattern is otherwise typical.

Syncranium. The premaxilla is comparable in form with that of *Haplochromis*, except that it is stouter, especially posteriorly, and its dentigerous surface broader.

As noted above, the broad and greatly flattened dentary is unique amongst Lake Victoria cichlids (Fig. 8).

The neurocranium agrees closely with that of *Platytaeniodus* and with *Haplochromis* of the " *crassilabris* " species-group (see p. 316).

Pharyngeal bone with a triangular and approximately equilateral dentigerous surface; pharyngeal teeth cuspidate, the median series often enlarged.

Scales ctenoid, lateral line interrupted, with 31 (f.1), 32 (f.10), 33 (f.38), 34 (f.14) or 35 (f.1) scales. (Hilgendorf (1888) gives L.S. 30 [probably on a mid-lateral series] for the holotype.) Cheek with three or four series of imbricating scales. (Hilgendorf [*loc. cit.*] gives 4–5 rows); 7–8 scales—rarely 6—between lateral line and origin of dorsal fin; 8–9, less commonly 7, between pectoral and pelvic fin bases.

Fins. Dorsal with 24 (f.4), 25 (f.45) or 26 (f.13) rays, comprising XV–XVII 8–10 spinous and soft rays. Two specimens have the formulae XIV 8 and XVII 6, but there are indications that these are the results of wounding and subsequent irregular healing. Anal with 11 (f.6), 12 (f.54) or 13 (f.4) rays, i.e. III, 8–10. Caudal fin truncate, scaled on proximal half only. Pectoral fin 23·9–33·0 (M = 28·4) per cent of standard length. Pelvics with first ray produced in both sexes but proportionately longer in adult males.

Coloration. Colours of preserved specimens are variable. *Adult males:* dark grey to black, median fins dark, caudal colourless or maculate; pelvics black. *Females and immature males:* light olive brown to silver, all fins yellow or colourless. Sometimes faint traces of transverse bars, an interrupted band below insertion of dorsal fin and a well-marked mid-lateral stripe.

Colours in life. Adult males: ground colour dark grey-green (darkening to deep slate-grey immediately after death), chest and branchiostegal membrane black. Dorsal fin dark grey-green, lappets red; red spots, often coalescing into streaks, between the rays. Caudal with proximal third to half black, distal part red. Anal with dark base, remainder red; ocelli yellow. Pectoral colourless; pelvics black, with faint red flush along median rays. *Adult females:* ground colour light olivaceous dorsally, shading through sulphur-yellow to pearly-white ventrally; usually two longitudinal bands as described above, of variable intensity. Lips yellow. Dorsal and caudal fins olivaceous; anal colourless or with slight yellow flush; small and ill-defined orange spots sometimes occur in the position of the male ocelli. Pelvics and pectoral fins yellow.

Three specimens (2 ♀, 1 ♂) from Bukakata, which were noted when discussing atypical dental patterns (p. 321), also exhibit aberrant coloration. This is known only from preserved material, in which it has the form of three large and elongate black spots, arranged mid-laterally, on a light ground colour.

Almost completely sex-limited polychromatism occurs in this species and, as in *M. bicolor*, it is the female which usually exhibits atypical coloration. Besides the black and yellow piebald, as described for *M. bicolor*, there is a second and more colourful, if less distinctive, pattern. Any attempt to describe this pattern must perforce be imprecise, since intensity and detail show a remarkable range of individual variability. The ground colour is invariably a light sandy-yellow, with a superimposed orange flush, usually most intense on the head. Dorsally there are a number of irregular and ill-defined dark blotches, separate or confluent, which occasionally extend on to the flank. In some individuals this dorsal pigmentation is comparable with the clearly defined blotches of a typical *bicolor* pattern; in others it is more diffuse and individual elements are only faintly discernible. The whole body, including the fins, is also peppered with small melanophores, particularly on the head and opercula. Fin coloration is extremely variable, but the caudal and anal are usually flushed with bright orange.

Sampling bias in favour of atypically-coloured individuals undoubtedly occurs and precludes the accurate estimation of frequency. Of thirty-five females examined, thirteen were " *bicolor* " and eleven of the other pattern. Polychromatism is known in populations from most areas in which the species has been collected.

A single male (119·0 mm. S.L., Busongwe, Kagera River area) had an incipient *bicolor* pattern, resembling in appearance and degree of pigmentation one of the " *bicolor* " males of *M. bicolor* (p. 309).

The genetical basis of, and selection factors maintaining polychromatism in *H. retrodens* remain undetermined, as previously explained in the case of *M. bicolor.*

Ecology

H. retrodens is widespread throughout Lake Victoria (see below). Sampling in many habitats shows the species to be restricted to littoral and sub-littoral areas, especially where the substrate is hard, and usually where there is submerged vegetation. The majority of specimens was caught in water from twelve to twenty feet deep, with a few from slightly deeper water.

Food. The gut contents of sixty-five individuals (size-range 75·0–144·0 mm. S.L.) have been examined; of these, only seven were empty. Mollusca (particularly Lamellibranchiata) are the predominating food, being recorded from thirty-six fishes. The majority of Mollusca is represented by finely broken shells. Insecta (f.8)—especially Ephemeroptera, Trichoptera and Chironomidae—together with Crustacea (f.3) and Hydracarina (f.2) occur less frequently. In fifteen fishes the ingested material consisted almost entirely of fragmented plant epidermis, whilst eleven others contained only sand grains or organic mud.

Observations made on fishes living in aquaria show that *H. retrodens,* when feeding, repeatedly makes short, darting movements into or over the substrate, the broad and horizontal mouth serving as a scoop or shovel. Much bottom material is spilled from the mouth or with the exhalent current. Snails were retained and apparently crushed within the jaws before being passed back to the pharynx. The presence of macerated plant epidermis in several fishes may be explained either as ingested bottom debris, or as the result of the fish actively scraping the leaves and stems of submerged plants, for which purpose the multi-seriate dentition would seem adapted. It may be significant to note that the frustules of epiphytic diatoms found in the stomachs of these fishes were empty, as were the epidermal cells which had been ruptured.

Breeding. No information is available on the breeding habits of *H. retrodens.* The smallest sexually mature individual was a female of 96 mm. S.L. (Bukakata, Uganda).

Affinities

Morphologically, *Hoplotilapia retrodens,* like *P. degeni* is relatively far removed from any Lake Victoria *Haplochromis* species or species group. Neither is it closely related to the other monotypic genera of that lake. Regan's remark (1922, p. 159) that " A remarkable group of three species includes *Haplochromis sauvagei* and the monotypic genera *Macropleurodus* and *Hoplotilapia*, which scarcely differ from each other except for the considerable differences in dentition, . . . " is difficult to endorse, unless the various structures whose forms are modified in association with the dentition and feeding habits are included in the term " dentition ". *Macropleurodus* and *Hoplotilapia* have manifestly dissimilar jaw morphology and also differ in the form of the neurocranium. These structural differences impart a characteristic physiognomy to the species, which allows them to be recognized without reference to the dental form and pattern. The occurrence of " *bicolor* " patterns in both *M. bicolor* and *H. retrodens* is suggestive, but at present little importance can be attached to this character since it occurs in at least three widely divergent species of *Haplochromis* as well as in *M. bicolor.* If neurocranial form can be considered as being of phylogenetic value, then the affinities of *Hoplotilapia* lie with the *H. crassilabris* species group, although *H. retrodens* has departed considerably from this complex in the form of its jaws and dental pattern.

Hoplotilapia and *Macropleurodus* show interesting trophic parallels, both between the two genera and in relation to the three mollusc-eating cichlids of Lake Victoria, viz. *Astatoreochromis alluaudi*, *Haplochromis pharyngomylus* and *H. ishmaeli.* Ecologically, *Hoplotilapia* and *Macropleurodus* occur together with *A. alluaudi* and *H. pharyngomylus*, but the diet of *Hoplotilapia* and especially of *Macropleurodus*, unlike that of the two last-named species, includes a substantial number of insects.

The parallelism between *Hoplotilapia* and *Macropleurodus* extends to the method of feeding, and particularly the manner in which the hard-shelled prey is crushed. It is this characteristic which most clearly emphasizes the morphological disparity between the two genera under discussion on the one hand and the three mollusc-eating species on the other ; these latter species, although including a monotypic genus, have deviated less markedly from the generalized *Haplochromis* anatomy. Whereas in *Astatoreochromis alluaudi*, *H. ishmaeli* and *H. pharyngomylus* the food is crushed entirely by means of the hypertrophied pharyngeal bones and teeth, in *Hoplotilapia* and *Macropleurodus* the food is broken mainly by the peculiarly developed jaws and oral dentition, although the relatively poorly-developed pharyngeal mill doubtless continues the process.

Despite functional similarity in the jaws and dentition of *Hoplotilapia* and *Macropleurodus*, there is considerable divergence in the detailed morphology of these elements. On the one hand, in *Macropleurodus* the jaws are short and stout, with a narrow gape ; associated with the stout supporting skeleton, the teeth are strong. On the other hand, the dentary and premaxilla of *Hoplotilapia*, although broad and encompassing a wide gape, appear relatively fragile. The dentition of *Hoplotilapia*, when compared with *Macropleurodus*, is seen to be composed of small and slender teeth which are arranged in bands broader both anteriorly and posteriorly than the corresponding teeth of *Macropleurodus*. Since the shells of Gastropoda in Lake Victoria are stouter than those of Lamellibranchiata, it would not be unreasonable to suppose that the strong, laterally concentrated and enlarged teeth of *Macropleurodus*, and the uniformly multi-seriate, finely-pointed teeth of *Hoplotilapia*, are associated with the predominantly gastropod diet of the former species, and the predominantly lamellibranch diet of the latter.

Study material and distribution records

Museum and Reg. No.	S.L. (mm.)	Locality.	Collector.
British Museum (Nat. Hist.) :			
1906.5.30.417–418	90 and 106	Buganga (Uganda)	Degen
1909.5.4.16	112	Sesse Is. (Uganda)	Bayon
1911.3.3.34	144	Jinja, Ripon falls (Uganda)	,,
1928.5.24.489–492	125–132	Lake Victoria	Graham
Genoa Museum :			
C.E.12.995 (holotype of *P. polyodon*)	135	—	—
C.E.12.994	112	—	—
B.M. (N.H.) :			
1955.2.10.141, 147–149	128–142	Rusinga Is. (Kenya)	E.A.F.R.O.
1955.2.10.145	129	Homa Bay (Kenya)	Ditto
1955.2.10.142–144, 146	105–135	Kamaringa (Kenya)	,,
1955.2.10.137–140	104–117	Kisumu (Kenya)	,,
1955.2.10.116–123, 180	76–138	Jinja (Uganda)	,,
1955.2.10.177–178	55	Beach nr. Nasu Point (Buvuma Channel, Uganda)	,,
1955.2.10.170–171	105 and 107	Pilkington Bay (Uganda)	,,
1955.2.10.176	114	Ramafuta Is. (Uganda)	,,
1955.2.10.168–169	155	Yempita Is. (Rosebery Channel, Uganda)	,,
1955.2.10.124–132	117–124	Harbour, Entebbe	,,
1955.2.10.133	109	Bugonga beach, Entebbe	,,
1955.2.10.172–175	96–142	Old Bukakata (Uganda)	,,
1955.2.10.150–163	104–132	Busongwe (Kagera R. mouth, Uganda)	,,
1955.2.10.179	127	Beach south of Bukoba (Tanganyika)	,,
1955.2.10.164–167	106–117	Majita beach (Tanganyika)	,,
1955.2.10.134	86	Harbour, Mwanza (Tanganyika)	,,
1955.2.10.135–136	74 and 139	Capri Bay, Mwanza (Tanganyika)	,,

Graham (1929) lists the distribution of *H. retrodens* as follows :

Kenya Colony : Mbita passage ; Kavirondo Gulf ; Kadimu Bay.
Tanganyika Territory : Mussonya Bay (Ukerewe Is.); trawl near Bukoba.

PARALABIDOCHROMIS gen. nov.

Diagnosis

Cichlid fishes of the *Haplochromis* group, but differing from that genus in having the anterior teeth in both jaws procurrent and disproportionately longer than the adjacent lateral teeth. Jaws narrowing at the symphysis ; lips thickened. Known only from Lake Victoria.

Type species : *Paralabidochromis victoriae* sp. nov.

The single specimen of *Paralabidochromis* available provides an interesting taxonomic and phylogenetic problem. No characters have been found which will distinguish this fish generically from specimens of the genus *Labidochromis* Trewavas ; a genus otherwise known only from Lake Nyasa. Unfortunately comparisons must be limited to characters apparent in preserved material and then only to the few specimens available. Nothing is known of the coloration in life of adult males in either genus. This is regrettable since coloration might well provide a reliable indication of the affinities of the two genera, both in relation to one another, and to the species flocks of Victoria and Nyasa (*vide* Regan, 1921, 686). The presence of a dark sub-marginal band on the dorsal fin of *Labidochromis vellicans*, in contradistinction to its absence in *Paralabidochromis* is probably of some importance. A sub-marginal band is not known in any Lake Victoria *Haplochromis* species, but is present in most species of the group of Nyasa genera to which *L. vellicans* is apparently related (*vide* Trewavas, 1935, p. 71).

Although on purely morphological grounds it might seem advisable to include the Lake Victoria species within the genus *Labidochromis*, such a decision would imply phyletic relationships between the Victoria and Nyasa species closer than those between either species and others of its own lake. To avoid this I have given greater weight to the difference in colour-pattern than would perhaps have been justified if both inhabited the same lake.

Apart from the presence of the pan-African genera *Tilapia* and *Haplochromis*, there is no obvious relationship between the Cichlidae of Lakes Nyasa and Victoria. Superficial resemblances between individual species, or genera, in the two lakes have been associated with differences which point to their being examples of convergent evolution (Regan, 1922, p. 159), although it would perhaps be preferable to consider this convergence of morphological characters as parallel evolution since the phenomenon occurs between species within a group of related genera.

It would seem most probable, therefore, that *Paralabidochromis* represents a remarkable example of exact and detailed parallel evolution with *Labidochromis*. Apart from the enlarged anterior teeth, neither *Labidochromis* nor *Paralabidochromis* departs greatly from the generalized *Haplochromis* type, as represented in the rivers of East and Central Africa. Thus, it is possible that the two genera were independently evolved from different parental *Haplochromis* species, which, however, shared the generalized facies of fluviatile species.

Paralabidochromis victoriae sp. nov.

FIG. 10.

Description

Depth of body 33·0; length of head 31·6 per cent of standard length. Dorsal profile of head and snout slightly curved and sloping moderately steeply. Preorbital depth 16·7 per cent of head length; interorbital width 25·0, snout length 33·4, diameter of eye 29·2 and depth of cheek 20·8 per cent of head length. Caudal peduncle 1·33 times as long as deep, its length 15·8 per cent of standard length.

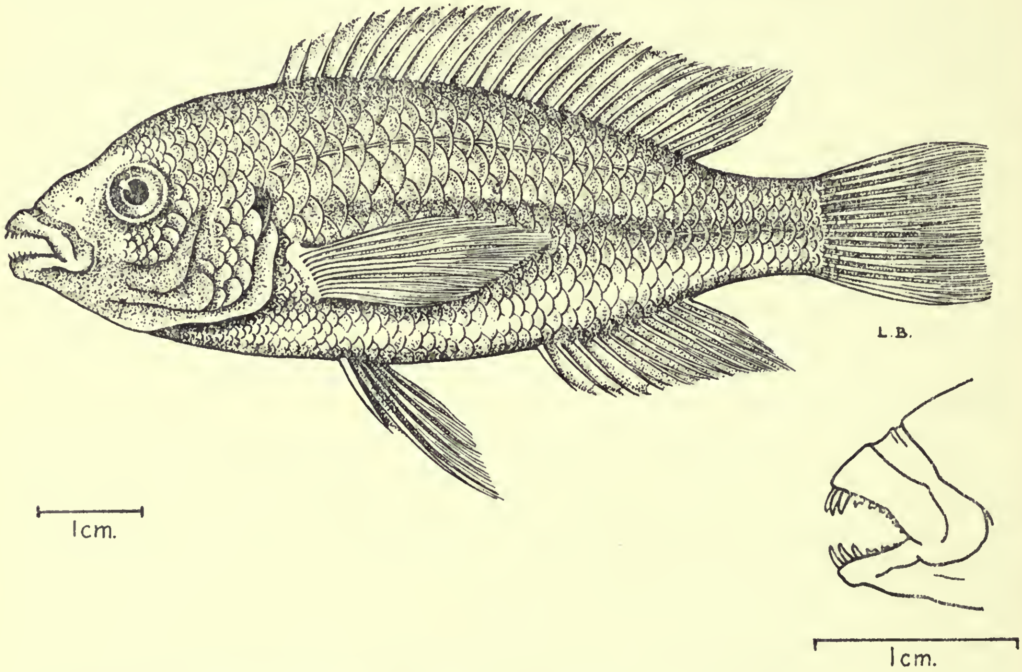


FIG. 10.—*Paralabidochromis victoriae*, ♂, holotype. Drawn by Miss L. Buswell.

Mouth almost horizontal, lips well developed. Posterior tip of the premaxilla extending to a point nearer the nostril than the anterior orbital margin. The angle between the rami of each jaw is acute giving a beak-like appearance, which is enhanced by the peculiar dentition.

Dentition. Thirty-eight teeth in the outer series of the premaxilla; the six anterior teeth in both jaws procurrent, greatly elongate, slender, slightly recurved and dagger-like; movable (Fig. 10). Postero-lateral outer teeth small and unicuspid, becoming progressively larger and weakly bicuspid laterally. Inner series in both jaws composed of tricuspid and compressed teeth, of which there are three rows in the upper and four in the lower jaw; outermost row of inner teeth in both jaws, somewhat enlarged and standing slightly apart from the remaining rows.

Lower pharyngeal bone triangular, the teeth small and cuspidate, with only the median series slightly enlarged.

Gill rakers short ; seven on lower limb of first arch.

Scales ctenoid ; lateral line interrupted, with 32 scales. Cheek with 2 series of imbricating scales ; 6 scales between origin of the dorsal fin and the upper lateral line ; 7 between pectoral and pelvic fins. Nuchal scales not exceptionally small.

Fins. Dorsal, XV 8 ; anal, III 9. Pectoral fin 25·0% of standard length ; pelvics with the first soft ray produced and extending posteriorly to the third anal spine. Caudal truncate, scaled on proximal half only.

Coloration. Preserved specimen light brown, with indications of seven faint transverse bands on the flanks, and a dark lachrymal stripe. Pelvic fins black, all other fins colourless.

Type locality. Sandy littoral, near Nasu Point, Buvuma Channel.

Described from a single specimen, a male 76·0 mm. S.L. (91·0 mm. T.L.), collected by the author whilst seine-netting at night, 29th May, 1951.

Affinities

Paralabidochromis victoriae is closely related morphologically, to *Labidochromis vellicans* of Lake Nyasa, from which it differs principally in possessing large scales on the chest, cheek and nape. The dorsal profile of the head and snout in *L. vellicans* apparently differs from that of *P. victoriae*, in being straighter and more steeply sloping.

Amongst the *Haplochromis* species of Lake Victoria, *P. victoriae*, has some structural affinity with *Haplochromis chilotes*. Both species have short and narrow jaws, thickened lips and a certain similarity of dentition. For example, the teeth of *H. chilotes* are slender and elongate anteriorly, few in number and arranged in an acute dental arch. However, the disproportionately long and procurrent anterior teeth of *P. victoriae*, and the hypertrophied lips of *H. chilotes*, immediately serve as diagnostic characters. The phylogeny of *H. chilotes*, is at present, obscure, but the species would seem more closely related to the *H. crassilabris* species group in Lake Victoria, than to *Paralabidochromis*.

DISCUSSION

It is clear from Regan's analysis of the Lake Victoria Cichlidae, that he did not consider the monotypic genera far removed phylogenetically from certain *Haplochromis* species, a view which is strengthened by the additional data now available. Although the monotypic genera are readily defined by trenchant characters they retain fundamental affinities with the *Haplochromis* species of Lake Victoria. But the morphological differentiation which these genera have undergone creates an impression of greater divergence than is shown by other adaptive groups within the Lake Victoria species flock. Analysis of the diagnostic characters of the genera described here, shows that, in any one genus, the anatomical characters of the head are functionally related to the dentition. Further, the ontogenetic basis for most of these characters is probably attributable to differential growth and not to any large-scale qualitative change. Thus the first evolutionary steps involved may well have been relatively simple and similar, in the earliest stages, to those which initiated the often slight differences characterizing the greater number of *Haplochromis* species.

Despite fundamental inter-relationship, three of the four monotypic genera exhibit considerable inter-generic divergence in the characters affected by the peculiar development of their dentition. The degree of divergence and the means by which it has been effected in *Macropleurodus*, *Platytaeniodus* and *Hoplotilapia* are such that the genera cannot be related *inter se*. That is to say, these genera represent three independent evolutionary offshoots from the basic *Haplochromis* stock. The fourth genus, *Paralabidochromis*, shows least departure from the generalized *Haplochromis* condition, but must also be looked upon as having evolved independently.

A broad outline of the probable phyletic relationships within the *Haplochromis* species flock is perhaps necessary before attempting further discussion of the monotypic genera.

There are some Lake Victoria *Haplochromis* species which, when seen in isolation or when known only from a few specimens, might seem almost as distinctive as the monotypic genera. It is possible, however, to relate these outstanding species to others more typical of their particular adaptive group (mollusc eaters, piscivores, epiphytic-algal grazers, etc.). Furthermore, when larger series of specimens are examined, intra-specific variation is sufficiently high to reduce considerably any apparent inter-specific gap.

With few exceptions, specific differences amongst the *Haplochromis* are quantitative and generally consequent upon the differential growth of various syncranial parts. Qualitative differences, on the other hand, are usually those which can be related to, and are used in defining, adaptational groups. At both inter- and intra-group levels, qualitative and quantitative differences tend to be small and intergrading.

It is in both qualitative and quantitative characters that the monotypic genera depart most markedly from *Haplochromis* but, unlike the inter-group differences within the *Haplochromis* flock, the morphological gap is clear cut, and remains so even when large series of specimens are examined.

On this interpretation, *Hoplotilapia* and *Platytaeniodus* probably examplify the phenomenon of " quantum evolution " as described by Simpson (1944 and 1953). It is difficult to suggest any ancestry for these genera nearer than a present-day species group, *viz.* the *H. crassilabris* complex. Even at this level relationship is extremely tenuous, and based only on similarity of skull form, in itself probably an adaptational character and therefore of doubtful phylogenetic significance. The jaws and dental pattern are so dissimilar in *Hoplotilapia* and *Platytaeniodus* that one must consider the genera separately and not as elements of a single lineage.

Macropleurodus is less readily regarded as being a product of quantum evolution, and will be discussed later.

Simpson (1944) has noted that quantum evolution is usually associated with a shift from one adaptive zone to another, and that the interzonal populations or species would be relatively ill-adapted, unstable and short-lived. Thus, morphological discontinuity is generally observed between the parental and divergent lineages.

The morphological discontinuity existing between *Platytaeniodus* and *Hoplotilapia*, and between these two genera and *Haplochromis* has been demonstrated ; it is the more regrettable then that pertinent ecological data for *P. degeni* are both inadequate and confusing, so that it is difficult to equate the apparent morphological specialization of this species with any particular ecological niche. The food of *P. degeni* is virtually unknown, although inorganic material and scant but varied organic remains suggest bottom-feeding habits. A multi-serial and concentrated dentition, such as that of *P. degeni* may possibly have adaptive value, particularly if food must be freed from the substrate or if it requires trituration before digestion can be effected. (It should be noted that no *Haplochromis* has consistently yielded such baffling residua in the gut.)

Hoplotilapia retrodens is somewhat better understood. In this species food is predominantly Molluscan. The functional significance of the jaw structure and dental pattern in *Hoplotilapia*, particularly with regard to its observed diet of thin-shelled bivalves, has been discussed above (p. 325). From these characters and the predominance of Mollusca over the other food organisms it would seem that the essential elements of quantum evolution are fairly well defined in *H. retrodens*. That is to say, the species shows both morphological discontinuity and entry into an adaptive niche different from that of the presumed parental stock.

There is, of course, the possibility that *Platytaeniodus* and *Hoplotilapia* represent an early stage in quantum evolution and that these species may be relatively ill-adapted to existing ecological conditions. Their further evolutionary development or, alternatively, extinction, will therefore depend upon environment change effecting, or failing to effect, the realization of characters which at present could only be considered prospective adaptations (*sensu* Simpson, 1953, p. 188).

The slight and often indeterminable adaptive differences between *Haplochromis* species occupying the same ecological zone, together with numerous instances of inter-specific overlap in feeding habits, would seem to suggest that there is, and has been, only slight selection-pressure acting through competition for food. Thus the continued existence of *Platytaeniodus* and *Hoplotilapia*, like that of many closely related *Haplochromis* species, could be attributed to a period of decreased selection pressure.

Although *Macropleurodus*, like *Platytaeniodus* and *Hoplotilapia*, is separated from *Haplochromis* by a clearly defined morphological gap, the gap is of lesser degree. Whereas *P. degeni* and *H. retrodens* exhibit unique jaw morphology and dental patterns without departure from *Haplochromis* in tooth form, the basic dental pattern of *M. bicolor* is foreshadowed in two *Haplochromis* species, as is the form of the dentary. Only in tooth form and shape of the premaxilla does *M. bicolor* show great differentiation from *H. prodromus*. The latter species is morphologically closely related to *H. sauvagei*, a smaller species, which in turn shows departure from the basic *Haplochromis* type towards *H. prodromus*. In *H. sauvagei* and *H. prodromus* the outer teeth are relatively stout and, anteriorly, there are several rows of inner teeth ; the neurocranium and dentary of these species also approach the *M. bicolor* condition. Both species feed on Mollusca and Insecta, the very slight differences in the feeding habits of *H. prodromus* and *H. sauvagei* being attributable to the smaller size of *H. sauvagei*.

It is tempting, therefore, to consider the members of the series *H. sauvagei*-*H. prodromus*-*M. bicolor* as representing stages of a lineage, although the possibility of independent evolution of the same adaptive characters, cannot be ignored. Until more critical evidence is available for the phyletic relationship of these species, they may be regarded either as separate end points of different lineages, or as a " stufenreihe", or single phyletic line. The three species do illustrate the gross anatomical and functional stages through which *Macropleurodus* could have evolved, although the transition in shape of teeth from a typical *Haplochromis* to *Macropleurodus* is not represented in any living species.

The isolated position of *Paralabidochromis* in relation to the *Haplochromis* species of Lake Victoria was commented upon above.

Little information is available on the evolutionary relationships of *Paralabidochromis*. Although taxonomically isolated from *Haplochromis* the genus is nearer the *Haplochromis* stem than either *Hoplotilapia, Platytaeniodus* or *Macropleurodus*. In Lake Nyasa, Trewavas (1935 and 1949) considers *Labidochromis vellicans* as belonging to a group of nine genera (which group excludes *Haplochromis*), that, although lacking an absolute character to distinguish them, are more closely related to each other than to any other genus. Such grouping is impossible for the monotypic genera of Lake Victoria. Within this lake the divergent genera of the *Haplochromis* group must be considered as being distinct from one another, as well as from the parental stock.

SUMMARY

(1) The genera *Macropleurodus* Regan, 1922, *Platytaeniodus* Boulenger, 1906, and *Hoplotilapia* Hilgendorf, 1888, are redefined on the basis of new and fairly extensive collections. Similarly, the species *M. bicolor* (Blgr.) 1906, *P. degeni* Boulenger, 1906, and *H. retrodens* Hilgendorf, 1888, are redescribed.

(2) Generic and specific characters are discussed, with particular regard to ontogenetic changes. Information gained from small specimens shows that three species previously considered as *Haplochromis* must be added to the synonymies of *M. bicolor* and *P. degeni*.

(3) Comparative anatomical and osteological studies of the head indicate that *Hoplotilapia* and *Platytaeniodus* are not closely related to any extant *Haplochromis* species in Lake Victoria. Morphological stages leading to the syncranial type found in *Macropleurodus* are, however, represented by two endemic *Haplochromis* species. On the basis of syncranial morphology, it is clear that the monotypic genera are not closely related *inter se*.

(4) Apparently sex-limited polychromatism occurring in *Macropleurodus* and *Hoplotilapia* is described and discussed.

(5) A fifth monotypic genus, *Paralabidochromis victoriae* is described. This genus exhibits remarkably close morphological parallelism with *Labidochromis vellicans* from Lake Nyasa.

(6) Locality lists and notes on the ecology of the genera are given, together with observations on the feeding habits of *Macropleurodus* and *Hoplotilapia*.

(7) The evolutionary relationships of the four genera are discussed. It is suggested that *Hoplotilapia* and *Platytaeniodus* may represent the products of low-level quantum evolution.

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A REVISION OF THE HYDROID GENUS *PERIGONIMUS* M. SARS, 1846

ON THREE NORTHERN SPECIES OF *HYDRACTINIA*

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Pp. 335–362 ; *Pls.* 11–12 ; 2 *Text-figures*

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A REVISION OF THE HYDROID GENUS *PERIGONIMUS* M. SARS, 1846

By WILLIAM J. REES

SYNOPSIS

During the past century nearly forty hydroids have been referred at one time or another to the genus *Perigonimus* M. Sars. The type species was demonstrated to be a *Bougainvillia* in 1938, and the status of all the other " *Perigonimus* " spp. is now considered and their position determined in accord with modern ideas on classification. They are distributed between the Orders Anthomedusae (Athecata), Leptomedusae (Thecata) and Limnomedusae, the majority being referred to four families of the first-mentioned Order.

Some material of *Perigonimus vestitus*, determined by Allman, has been re-discovered in the British Museum and is found to belong to *Leuckartiara octona* (Fleming). The original drawings of Joshua Alder's *Perigonimus linearis*, also in the Museum, reveal the presence of oral tentacles on the manubrium of the newly-liberated medusa, thus confirming that *Bougainvillia flavida* Hartlaub is identical with it.

INTRODUCTION

In 1938, I published a partial revision of *Perigonimus* in so far as it affected the groundwork for a monograph of British medusae, later published by F. S. Russell (1953). The earlier revision facilitated the establishment of common names for both the hydroid and the medusa of British species, but did not indicate the position of many extra-territorial ones whose status needed to be clarified. In this revision the position of these remaining species is considered and the conclusions reached earlier for others are re-stated briefly.

Michael Sars (1846) described a new handsome hydroid from the Norwegian coast under the name *Perigonimus muscoides* and also gave a brief, but inadequate, description of the medusa which is liberated with four tentacles. Later Allman (1864*a*), in his revision of Bougainvillid and other hydroids, referred a number of them which could not be placed in *Bougainvillia* (because they did not produce Bougainvillid medusae) to this genus of Sars on the assumption that they were cogeneric. Thus *Perigonimus* came to represent a group of *Bougainvillia*-like hydroids, which, either did not give rise to *Bougainvillia* medusae or had fixed gonophores. Gradually the picture emerged that the medusae of most of these non-*Bougainvillia* species belonged to another family, the Pandeidae. Hartlaub (1897 and 1914) demonstrated that *Perigonimus repens* was the hydroid of " *Tiara pileata* ", now known as *Leuckartiara octona* (Fleming), and that another Pandeid, *Halitholus cirratus* Hartlaub, also had a *Perigonimus* hydroid. More recently Rees & Russell (1937) were able to link the *Perigonimus serpens* kinds of hydroids with two species of medusae also of this family. Further revision of *Perigonimus* was made possible by the discovery that the type species of *Perigonimus* gave rise to a *Bougainvillia* medusa (Rees, 1938). Consequently *Perigonimus* became a synonym of *Bougainvillia* and no longer available as a name for hydroids which could not be placed in the same genus or even the same family.

As *Amphinema* (i.e., *Stomotoca*) had already been established by Rees & Russell (1937) for the hydroids as well as the medusae of this genus, *Leuckartiara* (already re-established for the medusa phase) was adopted for the appropriate hydroids, and *Rhizorhagium* M. Sars re-established for non-medusa bearing species.

As already mentioned this left a number of " *Perigonimus* " species either not satisfactorily classified or left out of consideration, and, in the brief notes below, it has been thought desirable to indicate their present status and where possible to add new information.

THE SPECIES WHICH HAVE BEEN REFERRED TO *PERIGONIMUS*.

Perigonimus abyssi G. O. Sars

Perigonimus abyssi G.O. Sars, 1873, *Forh. Vidensk. Selsk. Krist.*, **1873** : 126, Tab. v, figs. 27–30.

The newly liberated medusa of this minute species becomes free with two opposite tentacles and two partly developed tentacles on the other perradial bulbs (Rees, 1938). It is a Pandeid and has been referred provisionally to *Leuckartiara* Hartlaub pending further knowledge of its possible relationship with medusae of the genera *Leuckartiara, Neoturris* or *Catablema.*

Perigonimus antarcticus Hickson & Gravely

Perigonimus antarcticus Hickson & Gravely, 1907, *Nat. Antarct. Exped.*, 1901–1904, *Nat. Hist.*, **3** : 1, pl. i, figs. 1–3 ; pl. iv, fig. 32.

This species was placed in *Atractylis* (synonymous with *Bougainvillia*) by Vanhoffen (1910) and in a new genus *Gravelya* by Totton (1930), but its affinities lie with *Rhizorhagium* M. Sars, to which genus it was referred by Stechow (1919) and by Rees (1938). This last mentioned genus seems to be well constituted for simple Bougainvillid hydroids with fixed gonophores, but its relationship to *Aselomaris* Berrill and *Garveia* Wright will have to be considered in a wider revision of the Bougainvillidae.

Perigonimus apicatus Brooks

Perigonimus (*Stomotoca*) *apicata* Brooks, 1884, *Zool. Anz.*, **7** : 711.

This is the name given by Brooks to the hydroid of *Stomotoca apicata,* now known as *Stomotoca dinema* (Péron & Lesueur). Mayer (1910, p. 113) referred this hydroid to *S. rugosa* Mayer, but the absence of an apical projection in the newly liberated medusa points to *S. dinema,* as does the name used by Brooks for his hydroid.

Perigonimus bitentaculatus (Wright)

Atractylis bitentaculata Wright, 1867, *Proc. R. Phys. Soc. Edinb.*, **3** : 45, pl. i, fig. 5.

This species was referred provisionally to *Perigonimus* by Hincks (1868), but Wright himself gives the best clue as to the relationships of his species in the following sentence: " They have the habit, like that of *Lar* (Gosse), of quickly and repeatedly bending down the body until the mouth is brought close to the surface on which the zoophyte grows."

This species has not been reported since it was found by Wright in a *Pecten* shell dredged from the Firth of Forth near Inch Keith. The characters of the hydranth with its two opposite tentacles strongly suggest that the hydroid is related to *Proboscidactyla* (*Lar* of Gosse) and should be placed in the same family. The possibility should not be overlooked that this species may prove to belong to *Pochella polynema* Hartlaub, the only other medusa of this family known to occur in British waters. I do not propose to create a new genus for this species, but merely note that its position appears to be in the family Proboscidactylidae of the Order Limnomedusae.

Perigonimus cidaritis Weismann

Perigonimus cidaritis Weismann, 1883, *Entstehung der Sexualzellen bei den Hydromedusen*, Jena, p. 117, pl. xii, fig. 10–11.

This hydroid has a well-marked pseudohydrotheca in which the bases of the tentacles are protected in tube-like extensions of the perisarc as in *Bimeria* and *Thamnostoma*. As the medusa is a Bougainvillid closely related to *Thamnostoma russelli* Rees and there is very little difference in the hydroids, *P. cidaritis* has been referred to *Thamnostoma* by Rees (1938).

Perigonimus cirratus Hartlaub

Perigonimus cirratus Hartlaub, 1914, *Nord. Plankt.*, Lief. 17, XII: 274, fig. 234.

Hartlaub (1914) gave the name *P. cirratus* to the hydroid of the medusa *Halitholus cirratus* which he described in the same memoir, presumably for the reason that it was then customary to adhere to a dual system of classification. There are now no legitimate reasons why the hydroid should not also take the name *Halitholus*.

Perigonimus coccineus (Wright)

Atractylis coccinea Wright, 1861, *Ann. Mag. Nat. Hist.*, (3) **8**: 130.

E. S. Russell (1907) is the only author who has reported this species since it was originally described by Wright. In 1938 I suggested that the species might prove to be identical with *Rhizorhagium roseum*.

Perigonimus confertus (Alder)

Eudendrium? confertum Alder, 1856, *Trans. Tyneside Nat. Fld. Cl.*, **3**: 103, pl. iii, figs. 5–8.

Allman (1859) placed this species in *Dicoryne* because of the peculiarities of the gonophores, an assessment which has been generally approved. Recently Vervoort (1946) used the name *Perigonimus confertus* for the first time for this species, although presumably aware that this name is synonymous with *Bougainvillia* and therefore no longer available. The name *Dicoryne conferta* has been the established name of this species since 1859 and I see no reason to change it.

Perigonimus decorans Schneider

Perigonimus decorans Schneider, 1897, *Zool. Jb.* Syst., **10** : 479.

Schneider's description is too inadequate even to indicate in what family this hydroid could be placed.

Perigonimus formosus Fewkes

Perigonimus formosus Fewkes, 1889, *Bull. Essex Inst.*, **21** : 102, no figure.

Some small thumb-nail sketches of this species have been given by Fraser (1937, p. 35, pl. v, fig. 20) ; they indicate that *P. formosus* should be placed in *Rhizorhagium* M. Sars. A new description, especially of the gonophores, is much needed to determine the relationship of the species to *R. roseum.*

Perigonimus gelatinosus Duerden

Perigonimus gelatinosus Duerden, 1895, *Sci. Proc. R. Dublin Soc.*, N.S., **8** : 325, 327, pl. xiv, figs. 2-3.

Duerden's species is not identifiable with certainty with any known British species, although there is a possibility that it is identical with *Leuckartiara octona* as supposed by Hartlaub (1914). The complete retraction of the hydranth within the pseudohydrotheca could be due to poor preservation and by itself is no indication of specific differences.

Perigonimus georginae Hadzi

Perigonimus georginae Hadzi, 1913, *Rad. Jug. Akad. Znan. Umj.*, **200** : 98, figs. 7, 10 and 11.

The original description by Hadzi is not very satisfactory. He appears to have confused at least two species. His figure 7 is a *Stomatoca* hydroid, his figure 8 represents a *Bougainvillia*, and the newly liberated medusa, although combining some of the features of two species of *Stomotoca* medusae, cannot be referred with certainty to either *S. rugosa* Mayer or to *S. dinema* (Péron & Lesueur). Until the Adriatic medusae have been re-investigated it seems preferable to let this species retain its identity as *Stomotoca georginae.* The name *Dinema* applied by Hadzi to the medusa is a synonym of *Leuckartiara*, a member of a different sub-family.

Perigonimus (?) inflatus Duerden

Perigonimus (?) *inflatus* Duerden, 1895, *Sci. Proc. R. Dublin Soc.*, N.S., **8** : 329, pl. xiv, fig. 4.

This little known species does not seem to have been reported since Duerden's original description. It is here referred provisionally to *Rhizorhagium* M. Sars.

Perigonimus jonesii Osborn & Hargitt

Perigonimus jonesii Osborn & Hargitt, 1894, *Amer. Nat.*, **28** : 27, figs. 1–12.

I have followed Hartlaub (1914) in placing this species in the synonymy of *Leuckartiara octona* (Fleming). The colony described by Osborn & Hargitt compares favourably with those found on *Scaphander lignarius* in British waters.

Perigonimus linearis (Alder)

Atractylis linearis Alder, 1862, *Trans. Tyneside Nat. Fld. Cl.*, **5** : 230, pl. x, figs. 1–3.

Alder's *Atractylis linearis* was tentatively referred to *Perigonimus* by Allman (1864*a*). The newly liberated medusa has a very thick jelly and a small subumbrellar cavity, and in this it resembles *Bougainvillia flavida* Hartlaub (1897), an opinion later expressed by Hartlaub himself (1911). The published drawings of Alder do not suggest any oral tentacles on the manubrium of the medusa, but fortunately his original drawings (from which the engraving for his paper (1862, pl. x, figs. 2 and 3) was prepared) are preserved in the British Museum (Nat. Hist.), having been acquired by Canon A. M. Norman and later bequeathed by him. These drawings do show the oral tentacles faintly and so the two species can be regarded as identical.

Russell (1953) does not venture an opinion on the status of *P. linearis* or its medusa, but suggests that *B. flavida* may prove to be the hydroid of *Bougainvillia britannica*. Until this relationship can be demonstrated I propose to retain Alder's species under the name *Bougainvillia linearis* (Alder, 1862).

Perigonimus maclovianus (Lesson)

Perigonimus maclovianus Vanhoffen, 1910, *Dtsch. Sudpolar-Exped.*, **11** : 272, fig. 10*a–d* (hydroid).

The medusa of this species was described under the name *Cyanaea bougainvillii* by Lesson (1830), who later made it the type species of *Bougainvillia* under the name *B. macloviana* (1836). This is the name in common use to-day for both hydroid and medusa, although Vanhoffen (1910), who first described the hydroid, referred it to *Perigonimus*. Both Stechow (1919, p. 21) and Kramp (1928, p. 50) pointed out that *Bougainvillia* was the correct generic name for both hydroid and medusa.

Perigonimus minutus Allman

Perigonimus minutus Allman, 1863, *Ann. Mag. Nat. Hist.*, (3), **11** : 11.

Allman's *Perigonimus minutus* has been referred to *Leuckartiara octona* both by Hartlaub (1914) and Rees (1938). Allman's description and figures (1871–2, pl. xi, figs. 4–6) correspond closely with the slender polyps such as are commonly found on *Scaphander lignarius* (Rees, 1938, p. 14 fig. 3*d–f*).

Perigonimus miniatus (Wright)

Atractylis miniata Wright, 1863, *Proc. R. Phys. Soc. Edinb.*, **2** : 351.

Wright's *Atractylis miniata* was referred provisionally to *Perigonimus* by Hincks (1868). The reproduction of the species is not known, but the description suggests that Wright was describing a colony of *Rhizorhagium* and *R. roseum* in particular.

Perigonimus multicornis Allman

Perigonimus multicornis Allman, 1874, *Nature, Lond.*, **11** : 179.

A re-examination of Allman's type material in the Zoological Museum, Copenhagen by Kramp (1926) revealed that the species was *Eudendrium ramosum*.

Perigonimus muscoides M. Sars

Perigonimus muscoides M. Sars, 1846, *Fauna Littoralis Norvegiae*, Heft. **1** : 8, Tab. 1, figs. 19–21.

This is the type species of *Perigonimus* and the elucidation of its life history by Rees (1938, p. 2) revealed that its medusa was a *Bougainvillia, B. nordgaardi* (Browne, 1903). *Perigonimus* M. Sars, 1846, thus falls into the synonymy of *Bougainvillia* Lesson 1836 and the name *Bougainvillia muscoides* becomes applicable to both hydroid and medusa as demonstrated in the above paper.

Perigonimus muscus Allman

Perigonimus muscus Allman, 1863 ; *Ann. Mag. Nat. Hist.* (3), **11** : 12.

This species was referred to *Bougainvillia* by Allman (1864*a*). It was considered to be synonymous with *Bougainvillia ramosa* by Hartlaub (1911) and this view was confirmed by the studies of Brink (1925) who demonstrated that colonies passed through a *muscus* stage when young before reaching the stage typified by the usual *ramosa* kind of colony.

Perigonimus (?) nanellus Stechow

Perigonimus (?) *nanellus* Stechow, 1919, *Zool. Jb. Syst.*, **42** : 14, fig. C.

I consider this species to be a *Bougainvillia*, possibly representing a well formed colony of one of the common species, and pending further knowledge of its life history it is now referred to this genus as *B. nanellus*.

Perigonimus napolitanus Hargitt

Perigonimus napolitanus Hargitt, 1904, *Mitt. zool. Sta. Neapel*, **16** : 571, taf. 22, fig. 25.

This species is not recognizable.

Perigonimus nudus Stechow

Perigonimus nudus Stechow, 1919, *Zool. Jb. Syst.*, **42** : 16, fig. D.

The form of the hydranth as noted by Stechow resembles those of the medusa-bearing Campanopsinae of the family Haleciidae and the relationships of the species undoubtedly lie with this group rather than with any Athecate (Anthomedusan) group.

Perigonimus ? nutans Hincks

Perigonimus (?) *nutans* Hincks, 1877, *Ann. Mag. Nat. Hist.*, (4), **19** : 149, pl. xii, fig. 1.

Rees & Russell (1937, p. 71) regard this species as possibly a young polyp of the *Perigonimus serpens* type ; this kind of hydroid belongs to the genus *Amphinema*. There are two species in British waters, *A. dinema* and *A. rugosum*, and these are so alike that it is not possible to assign this species to one or the other.

Perigonimus palliatus (Wright)

Atractylis palliata, Wright, 1861, *Ann. Mag. Nat. Hist.* (3), **8** : 129, pl. iv, figs. 6 and 7.

In this species the pseudohydrotheca is large and dilated, but I do not think it has any special significance as a diagnostic character. The medusa, according to Wright

(1861) " resemble exactly those of *Atractylis* (*Perigonimus*) *repens* ", that is, *Leuckartiara octona* (Fleming). Wright's colony was on a shell inhabited by a hermit crab *Eupagurus bernhardus* and the size of the pseudohydrotheca can be attributed to habitat and feeding conditions as in the other colonies of *Leuckartiara octona* living under similar conditions (see Rees, 1938, p. 16, fig. 5). I regard the two species as identical.

Perigonimus pugetensis Heath

Perigonimus pugetensis Heath, 1910, *Biol. Bull. Woods Hole*, **19** : 74, figs. 1 and 2.

This small hydroid was found growing on a fish, *Hypsagonus quadricornis* (C. & V.) ; it was found that its newly liberated medusa was a Pandeid like *Leuckartiara octona.*

Hartlaub (1914) doubted whether the species was distinct from *L. octona*, and the latter has since proved to be a cosmopolitan species. Rees (1938) found a colony of *L. octona* growing on a fish, *Agonus cataphractus*, and this colony compared very favourably with that of Heath. It is now proposed to regard *P. pugetensis* as a synonym of *L. octona.*

Perigonimus pusillus (Wright)

Eudendrium pusillum Wright, 1857, *Edinb. New Phil. J.*, N.S., **6** : 84, pl. ii, fig. 8, 9.

Stechow (1919) revived the name *pusillus* for the better known name *Perigonimus repens* (Wright, 1858). It appears that Wright changed the name of his species to *repens* on the receipt of a paper by M. Sars (1857) in which he described a species of *Halecium* under the name *Eudendrium pusillum.*

Wright's species falls into the synonymy of *Leuckartiara octona* (Fleming).

Perigonimus quadritentaculatus (Wright)

Atractylis quadritentaculata Wright, 1867, *Proc. R. Phys. Soc. Edinb.* **3** : 45, pl. i, fig. 6.

This creeping form with long stolons and sessile, four tentacled hydranth is possibly a juvenile Bougainvillid, which cannot be identified with certainty with any particular species.

? *Perigonimus robustus* Fraser

? *Perigonimus robustus* Fraser, 1938, *Rep. Hancock Pacific Exped.*, **4**, No. 1 ; 17, pl. iii, fig. 12.

In the absence of information on the gonophore this species cannot be satisfactorily classified, and is therefore provisionally placed in *Bougainvillia.*

Perigonimus roseus (M. Sars)

Rhizorhagium roseum M. Sars, 1877, *Fauna Littoralis Norvegiae*, Heft **3** : 28, Tab. ii, figs. 37–43.

The genus *Rhizorhagium* was created for this species by Sars, and although the type species was referred for a time to *Perigonimus* by Bonnevie (1899) and others, the genus was re-instated by Rees (1938).

Perigonimus sarsii Bonnevie

Perigonimus sarsii Bonnevie, 1901, *Bergens Mus. Meeresfauna von Bergen*, Heft I, p. 6.

This species has been referred to *Rhizorhagium* by Rees (1938) and there is a distinct possibility that the species is founded on a colony of *R. roseum*, growing over the stems of another hydroid.

Perigonimus schneideri Motz-Kossowska

Perigonimus schneideri Motz-Kossowska, 1905, *Arch, Zool. exp. gén.*, (4), **3** : 72, fig. VI.

Stechow (1922) created a new genus *Perarella* for this species and indicated that its position was not in the Hydractinidae but rather in the Bougainvillinae near *Atractylis*.

Since then Komai (1931) has described the hydroid of the medusa *Cytaeis japonica*, to which the present species is clearly related. Both species have the following features in common : a reticulate anastomozing network of stolons, a short collar round the base of the hydranth, the hydranth itself long and tubular, of the *Podocoryne* type, and the gonophores borne singly on the hydrorhiza.

I propose to retain *Perarella* for Cytaeid hydroids in which there are fixed gonophores and to place the genus in the family Cytaeidae, L. Agassiz, 1862. Agassiz's definition excludes unrelated forms such as *Podocoryne* (including *Lymnorea*), *Turritopsis* and *Oceania*, which Uchida (1927) and others have placed in the family.

While possessing distinct oral *tentacles* on the manubrium of the medusa as in the Bougainvillidae, the presence of simple perradial tentacles together with the characters of the hydroid justify the existence of a separate family for *Cytaeis* and *Perarella*—a family in which the combined characters of hydroid and medusa present some characters in common with both the Hydractinidae and the Bougainvillidae, but none of their specialized features.

Perigonimus serpens Allman

Perigonimus serpens Allman, 1863, *Ann. Mag. Nat. Hist.* (3), **11** : 10.

Rees and Russell (1937) have referred this species to *Amphinema dinema* following the elucidation of the life history of this medusa and its hydroid. Allman (1871–2) clearly indicated in his illustrations of the medusa that he was dealing with this species and not with the closely related *A. rugosum*.

Perigonimus sessilis (Wright)

Eudendrium sessile Wright, 1857, *Edinb. New Phil. J*, N.S., **6** : 90, pl. iii, figs. 16–17.

This is the sessile form of *Leuckartiara octona* (Fleming). When the colony is growing on an uneven, constantly abraded surface the hydranths remain sessile in protected hollows or grooves and do not progress beyond the *sessilis* stage (Rees, 1938).

Perigonimus steinachi Jickeli

Perigonimus steinachi Jickeli, 1883, *Gegenbaurs Jb.*, **8** : 617, pl 27, figs. 1–9.

Jickeli gives a totally inadequate description of the morphology of his hydroid (although he discusses its histology at length) and it is not possible to indicate what it might be.

Perigonimus sulfureus Chun

Perigonimus sulfureus Chun, 1889, *S. B. Akad. Wiss. Berlin*, **1889** (2) : 524.

Stechow (1921 and 1923) created a new genus *Perigonella* for this species and placed it with the Hydractinians near *Stylactella*. Steche (1906) figures a well-developed medusa bud with conical bulbs with tentacles and manubrium devoid of oral tentacles, but we have insufficient information to assign this species to a family.

Perigonimus vagans Thornely

Perigonimus vagans Thornley, 1908, *J. Linn. Soc. Zool.*, **31** : 81, pl. ix, fig. 1.

This species is now referred provisionally to *Bougainvillia* pending the re-discovery of the hydroid. Thornely's description is insufficient to permit any other suggestions.

Perigonimus vestitus Allman

Perigonimus vestitus Allman, 1864*b*, *Ann. Mag. Nat. Hist.*, Ser. (3), **14** : 57.

In 1846 Allman described a new *Perigonimus, P. vestitus* from the Firth of Forth, in which, to quote his 1872 diagnosis the " posterior part of the body [of the hydranth], invested by the rough perisarc, which is thence continued as a delicate, smooth membrane over the remainder of the body nearly as far as the mouth ". His figures (1871, pl. xi, figs. 1–3) show the pseudohydrotheca (that is the perisarcal investment of the hydranth) to extend anteriorly beyond the tentacles close to the mouth. There is no suggestion that this perisarc is perforated to allow the tentacles to project (as they do) and no suggestion of any tubular perisarcal sheathing encircling the base of any tentacle. This seems to be one of the few occasions on which this far-sighted pioneer of hydroid systematics failed to make a satisfactory description.

Stechow (1919) referred *P. vestitus* to the medusa genus *Cytaeis* presumably on an assumed relationship between the hydroid and medusa of *vestitus* with *Perigonimus cidaritis*. There were no real grounds for this, as the figures demonstrate that *P. vestitus* gives rise to a typical Pandeid medusa, so that it must be stated that the species is related to genera like *Leuckartiara*, *Amphinema* and *Halitholus*.

In *Perigonimus vestitus* too, the bases of the tentacles are not enclosed in perisarcal tubes extending from the pseudohydrotheca itself. Such a feature is characteristic of *Bimeria*, *Thamnitis* and *Thamnostoma*, and the medusa of the latter clearly has affinities with the Bougainvillidae rather than the Pandeidae. *Cytaeis*, which Stechow erroneously associated with these Bimerid hydroids, belongs to none of these families.

Hartlaub (1914) in his revision of the Tiaridae had listed *Perigonimus vestitus* under the synonymy of *Leuckartiara octona*, but I was reluctant to follow him in my study of variation in the hydroid of this species (1938) in view of the diagnosis given by Allman. Fortunately, material of *Perigonimus vestitus* determined by Allman, growing on *Lepidochiton cinereus*, has recently been found in the collections of the British Museum (B.M. No. 1877.4.12.31).

A re-examination reveals that although the soft parts have disappeared the chitonous perisarc of the stems and pseudohydrothecae are still present. The latter are very similar in appearance to those that I described for a colony of *Leuckartiara octona* (Fleming) on *Corystes cassivelaunus* (Rees, 1938, p. 16, fig. 5). There is no suggestion of any perisarcal sheaths such as are found in *Bimeria*. The colonies exhibit no features that could not be found in a well-developed colony of *Leuckartiara octona*, and the characters of the medusa, as described by Allman, support this. For these reasons the species *vestitus* is placed in the synonymy of *Leuckartiara octona* (Fleming).

Perigonimus yoldiae-arcticae Birula

Perigonimus yoldiae-arcticae Birula, 1897, *Annu. Mus. Zool. Acad. St. Petersb.* **2** : 86, pl. x, fig. 3.

Jäderholm (1909) gives an excellent figure of this hydroid. I have examined material from the following localities :

Zoologiske Museum, Copenhagen.

Kandalakscha, on *Yoldia arctica*, 24 fm. (from St. Petersbourg Museum).

Riksmuseum, Stockholm.

Kandalakscha, 21–27 fm. Coll. N. Knipowitsch (from St. Petersbourg Museum).
Kandalakscha, 20–25 fm. Coll. A. Birula (from St. Petersbourg Museum).
Nordenskiold's Sea, 77° 1^1 N., 114° 35^1 E., 3.ix.1901 (Russian Polar Expedition, 1900–1903, St. 46).
Nordenskiold's Sea, 75° 42^1 N., 124° 41^1 E., 6.ix.1901 (Russian Polar Expedition, 1900–1903).
East Greenland, Franz-Josef Fjord (Muskoxfjord), 21.viii.1900, 220 m. (Swedish zoological Polar Expedition, 1900, St. 27).

All the material from the above localities is sterile. The pseudohydrotheca of the hydranth reaches almost to the tentacles, and in one hydranth it is a little loose-fitting and wrinkled which permits its limits to be seen. There is no indication of a web between the tentacles.

The most interesting (and also the characteristic) feature of this hydroid is the formation of ' nodes ' on the stems, and if we accept the belief that the species is a gymnoblastic hydroid (as seems most likely), these " nodes " indicate points of regeneration after periodic dying down of the hydranths. The species is referred provisionally to *Bougainvillia.*

SYNOPSIS OF THE STATUS OF THE DIFFERENT SPECIES OF " PERIGONIMUS "

Order ATHECATA (ANTHOMEDUSAE)

Family Cytaeidae	
Genus *Perarella* Stechow	(*Original name*)
Perarella schneideri	*Perigonimus schneideri* Motz-Kossowska
Family Bougainvillidae	
Sub-family Thamnostominae	
Genus *Thamnostoma* Haeckel	
Thamnostoma cidaritis	*Perigonimus cidaritis* Weismann
Sub-family Bougainvillinae	
Genus *Bougainvillia* Lesson	
Bougainvillia macloviana	*Perigonimus macloviana* Vanhoffen
Bougainvillia muscoides	*Perigonimus muscoides* M. Sars
Bougainvillia ramosa	*Perigonimus muscus* Allman
Bougainvillia linearis	*Atractylis linearis* Alder

Provisionally also:	
Bougainvillia nanellus	*Perigonimus* (?) *nanellus* Stechow
Bougainvillia robusta	*Perigonimus robustus* Fraser
Bougainvillia vagans	*Perigonimus vagans* Thornely
Bougainvillia yoldiae-arcticae	*Perigonimus yoldiae-arcticae* Birula
Bougainvillia sp.	*Atractylis quadritentaculata* Wright
Genus *Dicoryne* Allman	
Dicoryne conferta	*Eudendrium confertum* Alder
Genus *Rhizorhagium* M. Sars	
Rhizorhagium roseum	*Rhizorhagium roseum* M. Sars
	Perigonimus sarsii Bonnevie
	? *Atractylis coccinea* Wright
	? *Atractylis miniata* Wright
	? *Perigonimus inflatus* Duerden
Rhizorhagium antarcticum	*Perigonimus antarcticus* Hickson & Gravely
Rhizorhagium formosum	*Perigonimus formosus* Fewkes
Family Pandeidae	
Sub-family Stomotocinae	
Genus *Stomotoca* L. Agassiz	
Stomotoca dinema	*Perigonimus serpens* Allman
	Perigonimus (?) *nutans* Hincks
	Perigonimus apicatus Brooks
Stomotoca georginae	*Perigonimus georginae* Hadzi
Sub-family Pandeinae	
Genus *Leuckartiara* Hartlaub	
Leuckartiara octona	*Eudendrium pusillum* Wright
	Eudendrium sessile Wright
	Eudendrium repens
	Atractylis palliata Wright
	Perigonimus minutus Allman
	Perigonimus vestitus Allman
	Perigonimus jonesii Osborn & Hargitt
	Perigonimus pugetensis Heath
	? *Perigonimus gelatinosus* Duerden
Provisionally also :	
Leuckartiara abyssi	*Perigonimus abyssi* G. O. Sars
Genus *Halitholus* Hartlaub	
Halitholus cirratus	*Perigonimus cirratus* Hartlaub
Family Eudendriidae	
Genus *Eudendrium* Ehrenberg	
Eudendrium ramosum	*Perigonimus multicornis* Allman

Order THECATA (LEPTOMEDUSAE)

Family Haleciidae	
Sub-family Campanopsinae	
	Perigonimus nudus Stechow

Order LIMNOMEDUSAE

Family Proboscidactylidae	
Genus *Pochella* Hartlaub	
? *Pochella polynema*	*Atractylis bitentaculata* Wright

INCERTAE SEDIS

Perigonimus decorans Schneider
Perigonimus napolitanus Hargitt
Perigonimus steinachi Jickeli
Perigonella sulphureus (*Perigonimus sulphureus* Chun)

These few species which I have been unable to classify are insufficiently described.

The above classification is in accord with recent progress, but some of it may not be familiar to specialists who work only on hydroids and leave the medusa phase out of consideration. I believe with Allman (1864*a*) that "An adequate conception of the hydroid can thus only be obtained by regarding it as the product of two factors, one of them finding its expression in the trophosome, and the other in the gonosome". The result is frequently a mosaic, a blending of characteristics into a pattern which gives a much better picture of the position of the living species than does consideration of only a part of the life history.[1]

Much has been written by Kramp (1941 and 1949) about the dangers of attempting a single classification for hydroids and medusae, but its outlines are already apparent for the Anthomedusae, and this revision of *Perigonimus* is intended as a contribution towards it.

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ON THREE NORTHERN SPECIES OF *HYDRACTINIA*

By WILLIAM J. REES

(*With Plates 11–12*)

SYNOPSIS

Three species of *Hydractinia, H. allmani* Bonnevie, *H. carica* Bergh and *H. monocarpa* Allman from the Arctic are redescribed from numerous colonies. The great differences noted between colonies of the same species are shown to depend on the stage of reproductive exhaustion reached when the colonies were taken. What is known of their biology and distribution is summarized.

INTRODUCTION

Hydractinia is a large genus, and, of the many species which have been described, few have been worked on alive prior to a description being drawn up. In consequence many of the specialists who have worked on these animals (perforce from Expedition material) have seldom considered the specimens before them as having been something alive and constantly changing. Inevitably phases in growth and reproduction as well as ecological forms have on occasion been described as distinct species.

The northern *Hydractinia* species have been partially revised by Broch (1916) and Kramp (1932) so that there is now less confusion about the identity of arctic and subarctic forms. Some species however require redescription based on re-examination of as many colonies as possible in order to eliminate the use of so-called diagnostic features which are due to growth, seasonal variation, reproductive activities or reflect environmental conditions.

In species like *Coryne* where the gonophores are borne directly on the body of the hydranth, these reproductive activities cause the hydranth itself to be resorbed and often reduced to a mere stump without tentacles. This phenomenon may be termed reproductive exhaustion and it is by no means confined to the capitate hydroids where its effects are most noticeable. In *Hydractinia* reproductive exhaustion manifests itself first in the fertile polyps (or special reproductive polyps as the case may be) and also causes some reduction in the size of the nutritive polyps. I first noticed an appreciable reduction in the size of the sterile polyps in a Hydractinid due to this cause in the undescribed hydroid of *Podocoryne borealis*. During the fifteen days I had it under observation, it was producing large numbers of medusae, and by the time I was certain that it was distinct from the better-known *P. carnea*, the colony had altered so much in appearance that I could not honestly describe it in that condition (Rees, 1941).

This paper is confined to observations on three northern species, *Hydractinia allmani* Bonnevie, *Hydractinia carica* Bergh and *Hydractinia monocarpa* Allman, and is based on the rich arctic and subarctic collections of the Naturhistoriska Riksmuseum, Stockholm. Some of the material has been briefly described by Elof Jäderholm, but all the locality records of colonies in the Riksmuseum have been reported by him in various papers.

Hydractinia allmani Bonnevie

Hydractinia allmanii Bonnevie, 1898, *Z. wiss. Zool.*, **63** : 485, pl. xxvi, figs. 36–37.
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Kramp, 1914, *Medd. Grønland*, **23** : 988.
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Kramp, 1943, *Medd. Grønland*, **121**, No. 11 : 8.

TYPE LOCALITY. Norske Nordhavs Expedition 1876–78, St. 137, 67° 24′ N., 8° 58′ E., 827 m. (Zoological Museum, Oslo) Type locality selected here.

MATERIAL SEEN. In Riksmuseum, Stockholm :

Swedish Polar Expedition, 1900.
- St. 17, Mackenzie Bay, north of Franz Josef Fjord, E. Greenland, 12–35 m.
- St. 23, Mackenzie Bay, north of Franz Josef Fjord, E. Greenland, 3–10 m.
- St. 27, Muskoxfjord, Franz Josef Fjord, E. Greenland, 220 m.

Russian Polar Expedition, 1900–1903.
- St. 10 *d*, Kara Sea, 73° 27′ N., 79° 15′ E., 40 m.
- St. 18, Gulf of Middendorff, 75° 54′ N., 92° 59′ E., 12–14 m.
- St. 50, north of New Siberian Isles, 77° 20′ 30″ N., 138° 47′ E., 38 m.

Otto Torell : Bellsund, Spitzbergen, 8–12 fm.

SPECIFIC CHARACTERS. *Hydractinia* with encrusting base, with few simple, smooth spines. No tentaculozooids or spiral zooids. Nutritive polyps, long columnar (1·4–15·0 mm. high) with up to 16 filiform tentacles. Reproductive polyps (0·75–5·0 mm.) at first with hypostome and at least 8 tentacles becoming reduced to stumps with armed proboscis and even without tentacles. Usually one large and one small gonophore on each reproductive polyp.

Gonophores (0·6—1·4 × 0·5—1·3 mm.). Female, cryptomedusoid with 4 well-developed radial canals and 8 teat-like tentacle rudiments. Eggs numerous, polygonal at first becoming rounded or oval and escaping through a pore between the tentacle rudiments. Male gonophores also cryptomedusoid.

DISTRIBUTION. Apart from two records in rather deep water off the Norwegian coast, viz : position, 67° 24′ N., 8° 58′ W., S.W. of the Lofotens at a depth of 827 m. (Bonnevie, 1899) and position 63° 12′ N., 1° 30′ E., at a depth of 1320 m. (Broch, 1903), *H. allmani* has been found mainly in the high Arctic.

It has been found in the Spitzbergen area on a number of occasions (Bonnevie, 1899 ; Jäderholm, 1909 and Rylov, 1923). To the east the Russian Polar Expedition 1900–1903 took it in the Kara Sea, the Gulf of Middendorff and north of the New Siberian Islands (Jäderholm, 1908). In Greenland it was taken at three stations by the Swedish Polar Expedition, 1900, in the neighbourhood of Franz Josef Fjord (Jäderholm, 1902) and in Kempes Fjord by the Swedish Grönland Expedition, 1899. Other Greenland records from Hurry Fjord (Scoresby Sound area), Kempes Fjord, Vega Sound and the mouth of Forsblad Fjord are given by Kramp (1943).

The absence of records from the Okhotsk Sea and the Bering Sea are possibly due to lack of observations and the species may prove to be circumpolar in distribution.

DESCRIPTION. This is a large and handsome *Hydractinia*, but small and intermediate colonies occur and the species is very variable. For this reason several colonies are described below.

Fully grown colonies before the onset of reproductive exhaustion, as already mentioned above, are large and handsome and the following description is based on a colony from Muskoxfjord, East Greenland (Pl. 11, figs. 3–4). The encrusting base, which is continuous, has few spines, and arising from it are long spindly nutritive polyps reaching a height (to hypostome) of 8·0–13·5 mm. in preserved material. There is a well developed, conical proboscis, which is armed with a few nematocysts, with at its base, a circle of about 15 tentacles in a close double whorl. Each hydranth arises directly from the hydrorhiza and there is no distinct ring of perisarc at this point although the perisarc forms a thin wrinkled sheath.

The largest reproductive hydranths are 1·6–4·5 mm. high, that is, they are only about half the length of the nutritive ones, and from this colony it is not possible to say whether they are derived from nutritive polyps. The largest seen had a length of 4·5 mm.; it had a conical proboscis moderately well armed with nematocysts at its distal end. The tentacles were four in number and only 0·2 mm. in length. Some distance below the head of the hydranth it carried one large and one small gonophore. Other blastostyles ranged down to 1·6 mm. in height and the tentacles were sometimes reduced to mere knobs. Each blastostyle usually carried one large and one rudimentary gonophore. None of the gonophores was fully developed, the largest having a diameter of 1·4 mm. No spiral zooids have been observed.

Both male and female gonophores occur in the same colony. They are cryptomedusoids with well developed radial canals and the tentacle bulb rudiments are represented by four slightly pigmented areas (more mature gonophores are described from the colony taken at Mackenzie Bay, East Greenland on 1st August, 1900).

Another colony from Mackenzie Bay (also East Greenland) has similar gonophores, but the nutritive polyps are either less well developed or retracted (due to preservation methods) (Pl. 11, figs. 1 and 2). The polyps have a height of up to 5 mm. Likewise the gonophores are not fully mature and the blastostyles themselves are quite small being only 1·3–1·5 mm. in total height.

A second colony from Mackenzie Bay taken on 1st August, 1900, has distinctly smaller hydranths, these being less than 3·0 mm. in height, but both male and female gonophores are fully developed. The female gonophore is fully developed at 1·2 mm. in diameter and the tentacular rudiments are represented by 4 - 8 teat-like processes and the manubrium may protrude through the opening by which the eggs escape.

Another colony taken by the Russian Polar Expedition, 1900–1903, St. 50, north of the New Siberian Islands, is remarkable for the length of the nutritive polyps which are up to 14·3 mm. in height. The female gonophores are ripe (Pl. 11, fig. 7) and the male ones nearly so. The blastostyles vary from 1·5 mm. to 3·3 mm. in height and the larger carry 8 tentacles and the smaller ones only 1 or 2. Typically only 2 gonophores, one large and one small, are found on each blastostyle. The ripe female gonophore has 4 perradial rudiments of tentacles and 4 smaller interradial rudiments (Pl. 11, fig. 7).

The individual (both nutritive and reproductive) polyps of a colony from the Kara Sea are small. Some of the female gonophores are sufficiently advanced to show the rudiments of tentacle bulbs and radial canals. Here the blastostyles are more reduced than in some of the other colonies and often only one or two stumps of tentacles are left (Pl. 11, figs. 5 and 6). The proboscis of the reduced blastostyle is well armed with nematocysts. Eggs are numerous at first but become reduced in number to 10–15 in the ripe gonophore.

As will be noticed from Table I there is a considerable range in the size of the nutritive polyps and the very large size of the polyps in two colonies (one from Mackenzie Bay, St. 27 and the other from north of the New Siberian Islands) made me suspect that a different species was involved, but a careful re-examination of the material revealed no essential points of difference in any of the colonies except in size and degree of maturity of the gonophores.

TABLE I.—*Hydractinia allmani* Bonnevie.

(Measurements in mm.)

	Mackenzie Bay, E. Greenland			Gulf of Middendorff, Kara Sea	North of New Siberian Islands
	St. 17	St. 23	St. 27		
Length of nutritive polyp	2·4–2·7	1·4–3·1	7·0–13·5	2·0–2·2	3·1–12·0
Maximum diameter of polyp	0·4–0·5	0·2–0·4	0·5–0·9	0·2–0·7	0·7–0·9
Length of hypostome	0·5–0·6	0·3–0·4	0·6–0·8	0·3–0·35	0·5–0·8
Height of reproductive polyp	1·5–1·7	1·1–2·9	2·3–4·5	0·75–1·4	1·5–3·3
Length of gonophore	1·1–1·3	0·9–1·1	0·6–1·4	0·6–1·1	1·1–1·4
Diameter of gonophore	1·0–1·2	0·9–1·1	0·3–1·3	0·5–1·1	1·0–1·3

In these colonies the nutritive polyps are more than twice the size of the largest reproductive polyps; the latter have up to 8 tentacles and are very similar to the sterile polyps. It is not possible to be completely certain that they are reduced from the nutritive polyps through bearing gonophores, as in *Podocoryne carnea*, but it may be that we have here the beginnings of the specialization which results in the production of the specialized reduced reproductive polyps seen in *Hydractinia echinata*.

In the remaining colonies there is some overlap in the size of the two kinds of polyps, and in view of the small size of all the polyps it appears likely that they are reduced by prolonged breeding. This raises the question of the status of *Hydractinia ornata* Bonnevie, which, as far as I can see, is distinguished from *H. allmani* only on size ; its status must await the re-investigation of the original material.

There is one feature in the reduction of the reproductive polyp which is worth noting. The proboscis of the very reduced polyp is armed with nematocysts, these being concentrated at its tip as the tentacles are resorbed. The use of this character (an armed proboscis) in classification should therefore be used with caution.

BIOLOGY. In all records where the substratum of *Hydractinia allmani* has been indicated, the gastropod involved has been *Sipho curtus* (Jeffreys). In the high Arctic the hydroid occurs at depths of 3–760 m. in Greenland, 75–350 m. off Spitzbergen and in 12–40 m. in the more easterly localities.

Records of this species from off the Norwegian coast in comparatively deep water (*see* Distribution) suggest that this submergence is related to temperature. A colony reported by Jäderholm (1909, p. 49) was dredged from 350 m. where the bottom temperature was 2·73° C., while Bonnevie (1899, p. 11) recorded the species from bottoms where the temperatures were — 1° C. and — 1·2° C. Comparable temperatures (given by Ekman, 1953, p. 166) exist at the other localities at which this species has been found.

It is probable that *Hydractinia allmani* can be regarded as a stenothermal cold water species.

HISTORICAL AND RELATIONSHIPS. Since Bonnevie described the species in 1898, numerous records indicate that this is a common species in the high Arctic. It can be readily distinguished from *Hydractinia monocarpa* and *H. echinata* by its simple smooth spines ; from *Podocoryne* it is separated by its fixed gonophores. Compared with *H. carica*, it is more robust in habit, with longer polyps and more polyp-like reproductive zooids. The numerous eggs in the female gonophores (eggs are few in number in the gonophores of *H. carica*) also help to distinguish it.

Hydractinia carica Bergh 1887

Hydractinia carica Bergh, 1887, *Lütken, C.F. Dijmphna-Togtets zool.-bot. Ubbytte*, p. 331, pl. xxviii, fig. 1.
Schydlowsky, 1902, *Trav. Soc. Nat. Univ. Kharkow*, **36** : 114.
Hartlaub, 1905, *Zool. Jb. Suppl.*, **6**, Bd. **3** : 518.
Jäderholm, 1908, *Mém. Acad. Sci. St. Petersb.* (8) **18**, No. 12 : 8.
Jäderholm, 1909, *K. Svenska Vetens.-Akad. Handl.*, **45**, No. 1 : p. 48, pl. ii, figs. 10 and 11.
Broch, 1910, *Fauna Arctica*, **5** : 200.
Broch, 1916, *Danish Ingolf Expedition*, **5**, Part 6 : 48, pl. i, fig. 11.
Scheuring, 1922, *Wiss. Meeresuntersuch. Abt. Helgoland*, **13** : p. 168.
Rylov, 1923, *Annu. Mus. Zool. Acad. St. Peterb.*, **24** : 150, Taf. vi, figs. 2–3.
Fraser, 1931, *Contr. Canad. Biol.*, N.S., **6** : 6.
Uschakow, 1937, *Trans. Arct. Inst. Leningr.* **50** : 12.
Fraser, 1944, *Hydroids Atlant. Coast N. America*, p. 77, pl. xiii, fig. 53.

Hydractinia minuta Bonnevie, 1898, *Z. wiss. Zool.*, **63** : 468, pl. xxvi, fig. 38.
Bonnevie, 1899, *Norske Nordhavs Exped.* 1876–8, **26**, Zool. : 47 pl. i, fig. 3.
Bonnevie, 1901, *Meeresfauna von Bergen. Hydr.*, **1** : 7.
Broch, 1910, *Fauna Arctica*, **5** : p. 141 and 200.

Type locality. Petuchoffskoi Schar, Kara Sea, 15 m. (*Dijmphna Expedition*—Zoological Museum, Copenhagen).

Material seen. In Riksmuseum, Stockholm :

Fragment of type material on a mounted slide.
Bellsund, Spitzbergen, 20 fm. 22nd July, 1864 (A. J. Malmgren)
Bellsund, Spitzbergen, 8–12 fm. (Otto Torrell)
Recherche Bay, Spitzbergen, 13th July, 1898 (Spitzbergen Expedition, 1898)
67° 56′ N., 66° 18′ W., 13th October, 1897 (E. Nilsson)
Russian Polar Expedition, 1900–1903, St. 3, Murman Sea, 69° 35′ N., 50° 5′ E.; 70 m.

In British Museum :

Klaas Billen Bay, Spitzbergen, 28th July, 1921, C. S. Elton (Oxford Univ. Exped. to Spitzbergen, 1921).

Specific characters. *Hydractinia* with encrusting base with few high conical smooth spines (up to 0·7 mm. high) with rounded apices. Nutritive polyps, small, up to 2·3 mm. high when fixed, with a single whorl of 10–16 tentacles. Proboscis simple, almost unarmed. No spiral zooids known.

Reproductive polyps up to 2·3 mm. high, at first with conical hypostome and at least 8 tentacles, becoming greatly reduced to very short stumps without tentacles ; proboscis armed with nematocysts when present. Gonophores 3–7 in number borne in a ring round the polyp.

Gonophores cryptomedusoid, with 4 radial canals and rudiments of tentacles present but not developed into bulbs. Eggs large, 4–10 in number.

Distribution. *Hydractinia carica* is known from the Kara Sea (Bergh, 1887), the Barents Sea (Jäderholm, 1908 ; Scheuring, 1922), Spitzbergen, the Davis Strait area (West Greenland) and on the Norwegian coast in the neighbourhood of Bergen.

There are numerous records of this species from Spitzbergen, most of these being summarized by Jäderholm (1909) and Rylov (1923). I have been able to verify Jäderholm's record (1908) from Davis Strait and there are others by Fraser (1931 and 1944 as *carica* and *minuta*) from approximately the same area. The most southerly record is that of Bonnevie (1901) from the Hjeltefjord, Bergen as *H. minuta*.

There is insufficient information to hazard any opinion as to whether this species has a circumpolar distribution.

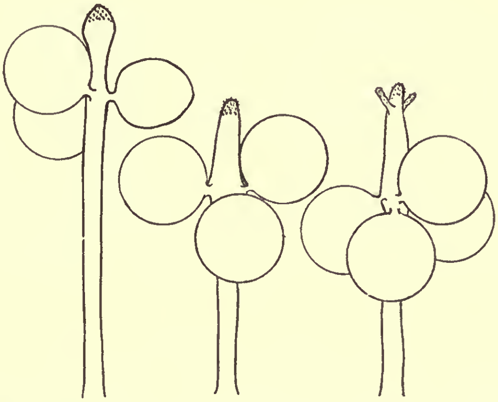
Description. This is an encrusting species with large spines but without small prickles. The large spines are simple, smooth and not sharply pointed ; they have no pore at the tip and in size range up to 0·7 mm. in length.

In preserved material the hydranths are tubular to fusiform in shape and may be over 2·0 mm. in height. The head of the hydranth is sometimes clavate and there is a conical proboscis without many nematocysts around the mouth. There are usually about 16 tentacles arranged more or less in a single whorl.

The reproductive polyps vary considerably from colony to colony according to the stage they had reached when taken, and it has been deemed desirable to describe them in the different colonies.

In the colony from Bellsund, Spitzbergen the reproductive polyps are completely reduced to very short stumps 0·17 mm. or less in length, bearing up to 5 gonophores each. These have diameters of about 0·45 mm. Sterile hydranths are 1·3–2·0 mm. in length.

Another colony from Recherche Bay, Spitzbergen, does not appear to have reached the same state of reproductive exhaustion as the one from Bellsund. In this colony the fertile polyps are still recognizable as polyps ; one of these still possessed 8 fully developed tentacles and a distinct proboscis and carried 5 moderately developed gonophores. Another reproductive polyp, with a height of 0·9 mm., had 7–8 tentacles and 4 gonophores each with a diameter of 0·3 mm.



Text-fig. 1.—*Hydractinia carica* Bergh : blastostyles from a colony from Recherche Bay, Spitzbergen (Swedish Spitzbergen Expedition, 1898).

A colony from position 67° 56′ N., 66° 18′ W., had particularly large blastostyles, 1·0–2·3 mm. in height to hypostome. These had 3–5 gonophores each and only a few had up to 2 reduced tentacles. The hypostome was usually well armed with nematocysts.

There were only a few very reduced polyps. These were so short that they could not be measured accurately ; they carried 5–7 gonophores and were clearly reaching the exhaustion stage.

Colonies from the Murmansk coast and Bellsund, Spitzbergen, were fertile and some of the reproductive polyps of these possessed 2 or more tentacles.

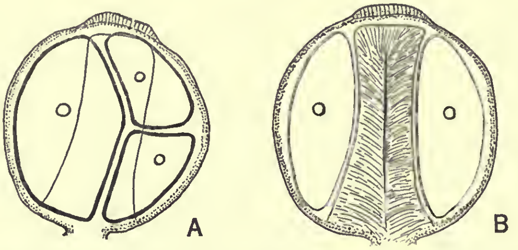
A mounted slide marked *Orig. Ex.*, Dijmphna Exp. presented by Levinsen appears to consist of part of the type material of this species. Measurements of this and other colonies in the Riksmuseum are given in Table II. Some of the reproductive polyps carry about 4 tentacles and others have lost them (Text-fig. 1).

TABLE II.—*Hydractinia carica* Bergh

(Measurements in mm.)

	Kara Sea (fragment of type material)	67° 56′ N., 66° 18′ W.	Bell Sound, Spitzbergen
Length of polyp	1·5–1·7	1·0–2·3	1·0–2·0
Maximum diameter of polyp	0·3–0·4	0·1–0·2	0·2–0·3
Length of hypostome	0·4	0·2	0·1–0·3
Height of reproductive polyp	0·75–0·9	0·1–2·3	0·17–0·2
Length of gonophore	0·28–0·4	0·3–0·4	0·45
Diameter of gonophore	0·25–0·4	0·3–0·4	0·45
Length of spine	—	—	0·37–0·7

Only female gonophores have been noted in this material; they are cryptomedusoids without radial canals but with apical patches of nematocysts. There is a well-developed manubrium and when ripe the gonophores contain 4–10 large eggs each (Text-fig. 2, *a*, *b*).



Text-fig. 2.—*Hydractinia carica* Bergh; gonophores from a fragment of the type colony, Kara Sea (Dijmphna Expedition): *a*, female gonophore; *b*, another female gonophore in optical section.

This material agrees with the earlier descriptions of Bergh (1887), Jäderholm (1908) and Broch (1916), but it has been possible to get a better picture of the species as a whole. The nutritive polyps (in preserved material) are seldom more than 2·0 mm. in height and it is possible that the reproductive polyps are derived directly from them. Bergh and the other authors indicated that the reproductive polyps might have 1–4 tentacles, but I have found 8 which supports my suggestion. Jäderholm (1909, pl. ii, figs. 10 and 11) gives good illustrations of partially reduced hydranths, and others are figured here (Fig. 1), but they may become so short that even the hypostome is almost completely reduced and the stalk below the point of origin of the gonophores also becomes extremely short. Broch (1916, p. 48) is undoubtedly right in his contention that Bonnevie's *H. minuta* (Bonnevie, 1899, p. 48) is identical with *H. carica*. I regard the colony she described as being in an advanced stage of reproductive exhaustion.

BIOLOGY. This species favours the shells of various northern species of *Buccinum* as a substratum. In the Barents Sea it has been found on *Buccinum undatum* and *B. tenue*. In the Spitzbergen area Jäderholm (1909) has found it on *Buccinum glaciale* and *Trophon clathrus*, while Rylov (1923) reported it as *H. minuta* on *Buccinum ovum* and *B. ciliatum*.

The bathymetric range appears to be 0–120 m. in the Spitzbergen area and 40–70 m. in the Barents Sea.

Hydractinia carica may be regarded as mainly a cold water species which, if Bonnevie's record from Bergen is authentic, is probably less stenothermal than *H. allmani.*

HISTORICAL AND RELATIONSHIPS. *Hydractinia carica* was described by Bergh (1887) from Petuchoffskoi Schar in the Kara Sea from a depth of 15 metres. Subsequently it was recorded many times in the far north and as *H. minuta* Bonnevie from Spitzbergen and elsewhere. As a species it is distinguished from other northern *Hydractinia* by its simple smooth spines, the extreme reduction which takes place in its reproductive polyps and by its gonophores. These have no radial canals and the female ones have few eggs.

Hydractinia monocarpa Allman

Hydractinia monocarpa Allman, 1874, *Nature, Lond.* **11**, No. 270 : 179.
Marktanner, 1895, *Zool. Jb.* (*Syst.*), **8** : 394.
Schydlowsky, 1902, *Trav. Soc. nat. Univ. Kharkow*, **36** : 114.
Hartlaub, 1905, *Zool. Jb. Suppl.* **6**, Bd. 3 : 518.
Jäderholm, 1908, *Mém. Acad. Sci. St. Petersb.* (8), *Cl. Phys.-Math.* **18**, No. 12 : 8, Taf. 1, fig. 6, Taf. 2, figs. 6–9.
Jäderholm, 1909, *K. Svenska Vetens.-Akad. Handl.* **45**, No. 1 : 49, Taf. ii, figs. 12–13.
Broch, 1910, *Fauna Arctica*, **5** : 141.
Broch, 1916, *Danish Ingolf Exped.* **5**, Pt. 6 : 47.
Rylov, 1923, *Annu. Mus. Zool. Acad. St. Petersb.* **24** : 148, Taf. VI, fig. 7.
Kramp, 1932, *Medd. Grønland*, **79**, No. 1 : 16.
Uschakow, 1937, *Trans. Arct. Inst. Leningr.*, **50** : 12.
Fraser, 1944, *Hydroids Atlantic Coast N. America*, p. 77.

Hydractinia echinata, Winther, 1880, *Naturh. Tidsskr.* **12** : 227, 254.
Levinsen, 1893, *Vidensk. Medd. naturh. Foren København*, 1892, p. 153.

TYPE LOCALITY. Spitzbergen, on *Trophon clathratus* L. (Allman, 1876) (Zoological Museum, Copenhagen)

MATERIAL SEEN. In Riksmuseum, Stockholm :

Matotschkim Schar, 15 fm. (Novaya Zemlya Expedition, 1875).
Russian Polar Expedition, 1900–1903, St. 53, 77° 10′ N., 142° 48′ E. (N. of New Siberian Isles) 35 m., on *Trophon clathratus* and *Bela plicifera.*

SPECIFIC CHARACTERS. *Hydractinia* with encrusting base with long, often irregular, hollow spines which may bifurcate distally. Spines longitudinally keeled especially at base, but smooth and not thorned, up to 2·4 mm. high. Nutritive polyps fusiform to tubular, up to 3·6 mm. high, borne on the encrusting base or on the sides of the spines. Tentacles, 10–15. Spiral zooids not known.

Reproductive polyps, up to 1·5 mm. high, with armed proboscis and at least 4 tentacles, or may be reduced without tentacles and greatly shortened. Gonophores 1–4 on each, but usually only one.

Gonophores : female, up to 1·4 mm. in diameter ; cryptomedusoid with 4 radial canals and apical patch of tissue. Male gonophores similar, up to 0·55–0·6 mm. in diameter.

DISTRIBUTION. All records of this species are from the high Arctic, chiefly from Spitzbergen, Novaya Zemlya and the New Siberian Isles. It appears to be a common species on shells at Spitzbergen (Allman, 1876 ; Jäderholm, 1909 and 1916 ; and Broch, 1910). The Russian Polar Expedition 1900–1903 took it at two stations off the New Siberian Islands and in Chatanga Bay in Nordenskjold's Sea (Jäderholm, 1908). Records from Novaya Zemlya are given by Jäderholm (1909).

West Greenland records from Upernivik and from near Cape Atholl are given by Kramp (1932). This distribution suggests that the species is circumpolar.

DESCRIPTION. This species has an encrusting base, but the most characteristic feature is the presence of long, upright irregularly-formed spines rising to a height of about 3 mm. (Pl. 12, figs. 8–11). The spines are seldom straight or symmetrical and are usually curved towards the tip which tapers to an open hyaline or horn-coloured tube. Frequently the spines are double or bifurcated and their surface is seldom smooth. The naked coenosarc may cover a good part of the spines.

The nutritive hydranths may be long and tubular reaching (when expanded) a considerable length. Some preserved examples, moderately well fixed, have a length of 3·6 mm., but, when contracted, may only be one-third or less than this length. Such retracted polyps are either cylindrical or flask-shaped (Pl. 12, figs. 9 and 10). The hypostome carries nematocysts, particularly near the tip, but they are few in number. There are 10–14 tentacles. A curious feature of this species is that one or more polyps may be carried on the spines themselves and I have seen up to three on one spine (Pl. 12, figs. 9 and 10).

The reproductive polyps, noted in the material seen, were up to 1·5 mm. in height and were provided with up to 4 tentacles. Each had an armed tip to the proboscis and carried up to 4 gonophores. Only female gonophores have been noted by me ; these are large, 0·5–0·7 mm. in diameter and are cryptomedusoids with manubrium and radial canals. It is clear that the blastostyles become considerably reduced due to reproductive exhaustion. Frequently they are reduced so much that the gonophores appears to be almost sessile on the coenosarc. When this happens the upper part of the polyp seems to become larger and more polypoid, but the stalk below the point of origin of the gonophore is extremely short.

In his original description Allman (1874) described the reproductive polyps as devoid of tentacles, but tentacles have been noted by Jäderholm (1908). Rylov (1923), Kramp (1932) and by myself. The diagnosis of the species (p. 25) differs greatly from that of Allman because more colonies have been available for study.

BIOLOGY. *Hydractinia monocarpa* has been found on the shells of gastropods such as *Trophon clathrus*, *Bela plicifera* and *Buccinum hydrophanum* (Jäderholm, 1908, 1916, and Kramp, 1932). The hydroid may grow all over the shell as in a specimen of *Bela plicifera* from Kol Bay, Isfjord, Spitzbergen. The nutritive and reproductive polyps flourish best in and near the sutures between whorls, but they also occur on exposed surfaces and are absent only on abraded surfaces of the shell. The tall spines are fairly closely grouped and must offer some protection to the zooids.

The species has a known bathymetric range of 14–165 metres, the deepest record being from West Greenland (Kramp, 1932). Most of the records from Spitzbergen and elsewhere in the Polar Sea are, however, from shallow coastal waters.

Hydractinia monocarpa may be regarded as a high Arctic or stenothermal cold water species.

HISTORICAL AND RELATIONSHIPS. *Hydractinia monocarpa* was described by Allman from a colony labelled " Spitzbergen " in the Zoologiske Museum, Copenhagen. It has since been found frequently in the Spitzbergen area and elsewhere in the high Arctic.

This distinctive species, with its long, hollow, often bifurcated spines, its polyps arising from both encrusting base and spines, its cryptomedusoid gonophores, with four radial canals but without tentacle rudiments, cannot be mistaken for any other northern species.

The presence of hydranths on the spines recalls the much greater development of this feature in *Hydrissa sodalis* (Stimpson) from East Asiatic seas.

ACKNOWLEDGEMENTS

I wish to thank Dr. Bengt Hubendick for hospitality while examining this material at the Riksmuseum, Stockholm, and also for the loan of some of it for more detailed examination in London. I also wish to thank Mr. M. G. Sawyers for the care he has taken in preparing the photographs of *Hydractinia allmani* and *H. monocarpa* from slides made by the late Elof Jäderholm.

DISCUSSION

Colonies of *Hydractinia allmani* show marked variation according to the stage of reproductive exhaustion reached at time of capture and it has been suggested here that the reproductive polyps in this species are derived from nutritive ones. The great variation in the size of nutritive polyps and in the reproductive polyps (from well formed ones to almost blastostyles) is highly significant, and implies that we must use these features with great caution in distinguishing species. It brings to mind the very large number of boreal and tropical species of *Hydractinia* which have been described on single colonies. A critical study of these must result in a great reduction in the number of recognizable species. Another feature, noted in this paper, is the concentration of nematocysts in the tip of the hypostome as the tentacles are resorbed during reduction of the polyp. It means that the armed proboscis, too, must be used with discretion as a diagnostic character.

The study of *Hydractinia carica* also bears out the general conclusions noted above, but this species is notable for the almost complete resorption of the reproductive polyp and shortening of its stem, so that the gonophores sometimes give the appearance of being sessile on the hydrorhiza and even the hypostome may disappear. This, too, is a factor to be considered in classification.

Although *H. monocarpa* can be readily distinguished by its spines, its reproductive polyps vary according to phase and bear out the general conclusions reached for the other two species.

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BRITISH MUSEUM

PLATE II

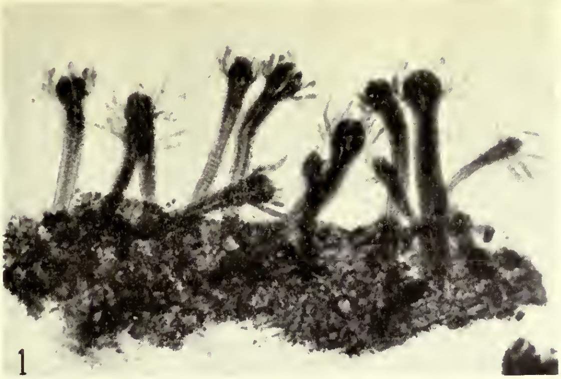
Hydractinia allmani Bonnevie

Figs. 1 and 2.—Fragments of a colony from St. 23, Mackenzie Bay, East Greenland (Swedish Zoological Polar Expedition, 1900); × 10.

Figs. 3 and 4.—Fragments of a colony from St. 27, Muskoxfjord, Franz Josef Fjord (Swedish Zoological Polar Expedition, 1900); × 5.

Figs. 5 and 6.—Reproductive zooids with female gonophores; St. 18, Karahavet, Middendorff's Sea (Russian Polar Expedition, 1900–1903); × 25.

Fig. 7.—Reproductive zooid with ripe female gonophore; St. 50, north of New Siberian Islands (Russian Polar Expedition, 1900–1903); × 14.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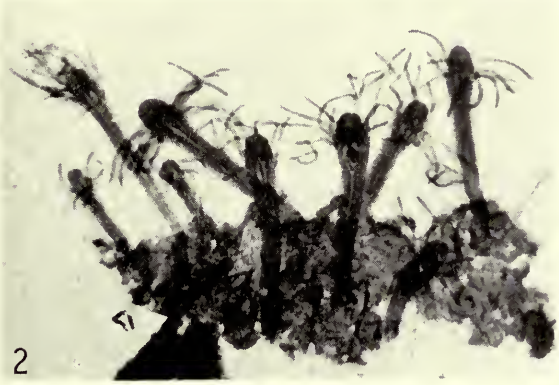
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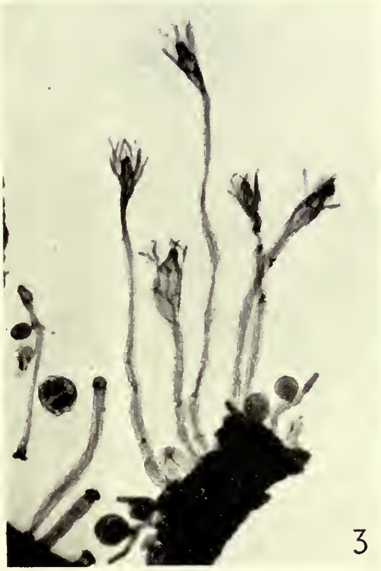
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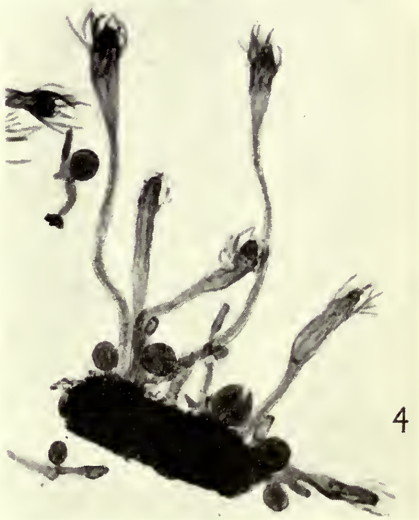
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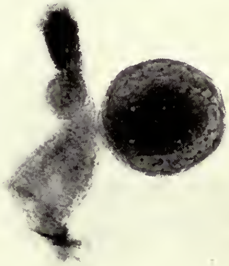
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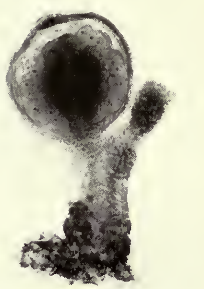
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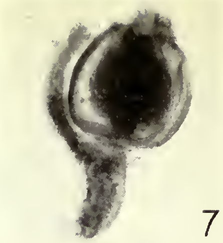
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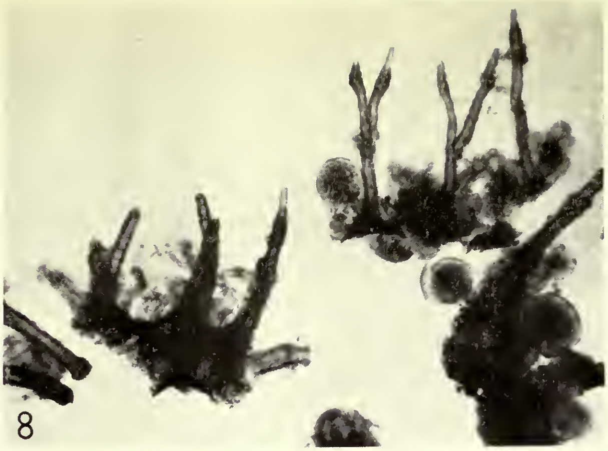
Hydractinia allmani Bonnevie.

PLATE 12

Hydractinia monocarpa Allman from St. 53, north of New Siberian Islands (Russian Polar Expedition, 1900–1903).

Fig. 8.—Spines and female gonophores; × 12.

Figs. 9–11.—Spines and nutritive polyps; × 20, × 21, × 25.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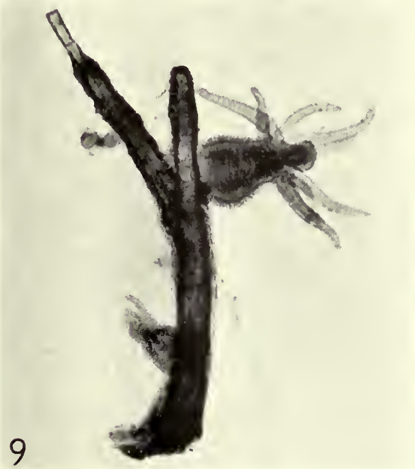
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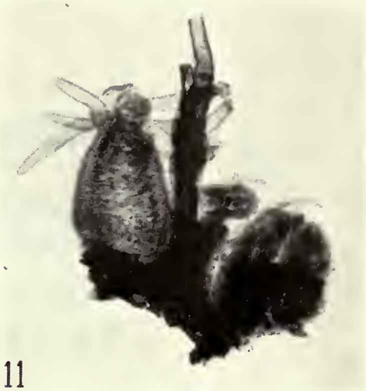
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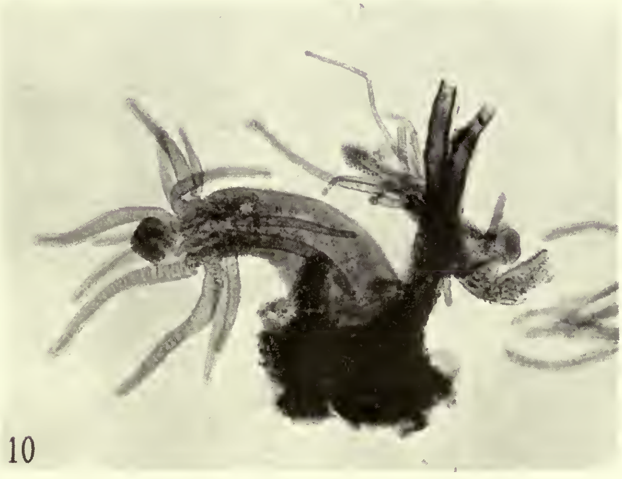
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Hydractinia monocarpa Allman.

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THE LIZARD GENUS

APRASIA

H. W. PARKER

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
ZOOLOGY Vol. 3 No. 9
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BY

H. W. PARKER

Pp. 363–385; 7 *Text-figures*

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THE LIZARD GENUS *APRASIA*;

ITS TAXONOMY AND TEMPERATURE-CORRELATED VARIATION

By H. W. PARKER

SYNOPSIS

The genus *Ophioseps* cannot be maintained ; its past recognition was due to errors of identification and observation. *Aprasia* is the most completely adapted of the Pygopodidae for fossorial life, the family exhibiting a continuous series in degeneration of limbs and girdles, with the development of a serpentiform habitus and cranial modifications for burrowing. There are three species with a combined range from Victoria to the Monte Bello Islands but which occur together in only a restricted area near Albany. Two of the species show a considerable range of variation in the numbers of presacral vertebrae and scales. This variation appears to be correlated with differing summer temperatures. Since the characters are meristic and such characters have been shown, in other cold-blooded animals, to be directly affected by the temperature prevailing during embryological development, it is suggested that the variation may prove to be thermoplastic. The other taxonomically useful, but non-meristic, characters show no significant variation in different climatic regions. The temperature correlated clines are discontinuous geographically, permitting recognition of two new subspecies.

Two small limbless lizards were collected on Hermite Island, one of the Monte Bello group, in 1952. They differ from any of the known species of the genus *Aprasia* but most nearly resemble *Aprasia repens* Fry. Since the Monte Bello Islands are geographically far removed from the recorded range of any species of *Aprasia* a re-survey of the known species of the genus, and its alleged ally *Ophioseps*, was necessary to ascertain the probable significance of the differences. More than 120 specimens were assembled for comparison, and this series covered not only the whole of the previously known geographical range, but included recently captured specimens from regions where none of these lizards had previously been reported.

MORPHOLOGY AND COMPOSITION OF THE GENUS

As will be demonstrated presently the series is subdivisible into five groups with morphological differences, but all the specimens share the following characters :

Scales smooth, subequal dorsally and ventrally except on the throat and pectoral region, where they are slightly smaller than on the belly ; 12 or 14 longitudinal rows of scales at mid-body. General habitus worm-like, the head and tail not being wider or narrower than the body, which is very elongate and cylindrical. The snout projects in front of the labial margin and the large rostral shield is visible from above; five supralabials, the first being wholly or partly fused with a large nasal shield, which forms a suture with its fellow behind the rostral; pre-frontals large, forming a median suture and in contact with the second labial; a small pre-ocular in contact with the third labial and the supra-ocular, which reaches the fourth supra-labial or is separated from it by a single small post-ocular; frontal hexagonal; parietals not much larger than the scales of the occiput and nape, not in contact behind the frontal. Eye covered by a circular brill edged with a ring of small granules. Shields and scales of the head beset with numerous minute pustules, presumably tactile sense-organs. No external auditory meatus, tympanum or tympanic cavity. No vestiges of fore-limbs externally; hind-limbs visible as small triangular flaps at the lateral corners of the vent, each being covered by a single triangular scale not very different in size or appearance from the other scales of the region. No pre-anal pores. A pair of post-anal sacs close behind the vent and opening by a pair of small pores just within its posterior border. Bordering the anterior margin of each of these sacs there is, in males, a post-cloacal bone which pierces the skin laterally close, but caudomesial, to the hind-limb vestige; the protruding portion is sometimes claw-shaped, with the free terminal part of the claw directed postero-dorsally, or sometimes subcircular in surface view (Text-fig. 1).

The skull of *Aprasia repens* has recently been figured by McDowell & Bogert (1954, fig. 21) and specimens of all the species represented in the present material (*vide infra*) have been found to conform to this pattern. There is a single pre-

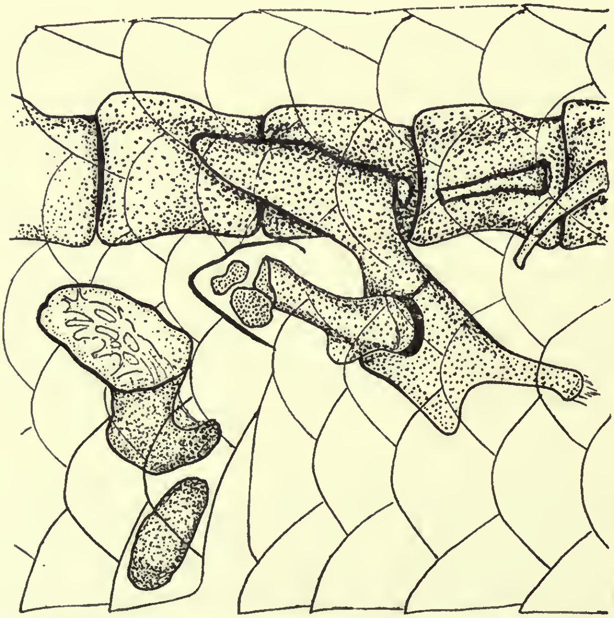

Fig. 1. Pelvic region of a cleared specimen seen in three-quarters ventro-lateral view from the right side to show hind limb, girdle and post-cloacal bones. (*Aprasia striolata*, ♂.)

maxilla; paired nasals form a long median suture; the prefrontals are separated mesially and extend posteriorly above the orbit to form a suture with a small postfrontal; the frontals are fused to form a single median element, but the parietals are paired, forming a long median suture; there is a narrow supra temporal (tabular).[1] In both sexes the maxillary is edentulous and the dentary is toothed; the premaxilla is toothed in adult males of all species, but is completely edentulous in juveniles of all species and also in females, except in *A. striolata* where vestigial teeth may be present. In the lower jaw the splenial is wanting or is fused with the prearticular. The only skull examined that deviates in any way from this pattern is the one figured and described by Jensen (1901) as *Ophiopsiseps nasutus* Bocage. This description has been the cause of much confusion. The lizard was incorrectly identified and the description is incorrect in many points that subsequent authors have accepted as indicating the existence of a genus (*Ophioseps* or *Ophiopsiseps*) distinct from *Aprasia*. As will be demonstrated presently (p. 380), the type specimens of the type species of *Aprasia* Gray and *Ophioseps* Bocage are conspecific and the two names are thus strict synonyms. But even apart from this nomenclatorial consideration there appear to be no grounds for the recognition of a second genus. Jensen's specimens have been compared with a series of others from the same geographical area (Victoria and S. Australia) and have been found to be juveniles of the one and only species that occurs there. This, in its adult phase, has a skull like that described above. Jensen was in error in several respects, notably in regard to the frontals, prefrontals, postfrontals and " squamosal " (supratemporal) which, despite the immaturity of the skull, do not differ from those of the adult. He was also misled by the absence of any median suture between the parietals into believing that these bones were completely fused; in fact, owing to immaturity, the development of the parietals is incomplete, but they exist as two very thin lateral blades widely separated on the mid-line.

Although all the species and subspecies examined have skulls that are essentially similar in their general structure, there will undoubtedly be found to be specific differences and, perhaps, ontogenetic differences in proportion. Insufficient skeletal material is available to the writer to permit of any definite conclusions, but in the long-snouted species (*A. repens*) the pre-orbital increase in length is accompanied by an increase in length of the nasals. Thus, the ratio of frontal to nasal length was found to be approximately 1·24 (c.f. also Bogert & McDowell's figure where the ratio is 1·25) in this species, but 1·40–1·49 in specimens from South Australia (*A. striolata*) and 1·50–1·56 in an example of *Aprasia pulchella* and the holotype of *Ophioseps nasutus* Bocage.

Other skeletal features of the series are as follows. Presacral vertebrae 88–137, the number varying from species to species; the first three vertebrae (four in one specimen) lack ribs; sacral vertebrae three, with sacral ribs diminishing in length caudad, the anterior two being free and the last knob-like and fused to the centrum (Text-fig. 2). Shoulder girdle a V-shaped structure composed of a pair of rod-like coracoids connected across the mid-ventral line by a V-shaped sternal cartilage. Each coracoid, which is slightly expanded at its ends, runs antero-dorsally from the sternum to a point near the distal extremity of the first rib. The dorsal end of each is tipped with a short, tapering length of cartilage which may represent a scapula. There are no traces of any bones of the fore-limb.

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[1] McDowell & Bogert (1954) figure this bone in their dorsal and ventral views (figs. 21A and B) but do not label it; it is not shown in the lateral view (fig. 21C).

The pelvis (Text-figs. 1 and 2) consists of a subtriangular, slightly curled ilium and an ischiopubis. The ilium articulates at its postero-dorsal corner with the third, knob-like, sacral rib and the other two sacral ribs have loose ligamentous connexions with its antero-dorsal border. The ischium and pubis are fused, the ischiadic portion of the combined bone being rectangular and the pubic portion rod-like; both portions are widely separated from their fellows on the mid-ventral line. The hind limb consists of a short, stout femur, with a well-developed trochanter, and a nodule-like vestige of a tibia; sometimes there is also a vestigial fibula.

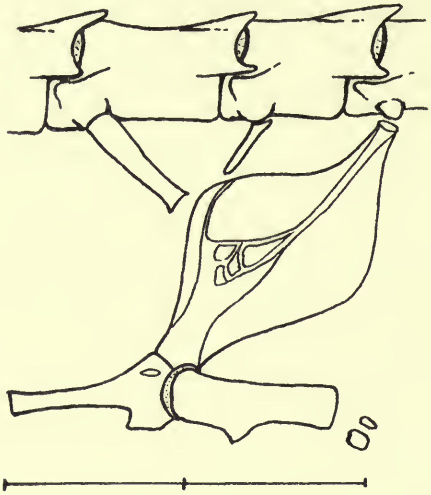

FIG. 2. *Aprasia striolata striolata*. Left pelvis and hind limb of a male, diagrammatic to show sacral connexions.

POSITION IN THE FAMILY PYGOPODIDAE

The various forms possessing these characters in common are clearly a closely related group and this position is best expressed taxonomically by treating them as a single genus. McDowell & Bogert (1954) in discussing the relationships of the family Pygopodidae have pointed out that " the more typical pygopods, the Pygopodinae and Lialinae " are akin to the geckoes in many features. But Jensen's account of *Ophioseps* misled them and, although they do not commit themselves definitely, they say " we see no reason to question Jensen's placing of *Ophioseps* in a distinct family, as Boulenger (1885) suggested. It is probable, however, that *Aprasia* should be transferred to the Ophiosepidae." Since *Ophioseps, sensu* Jensen, is a fallacy any such disposal of *Aprasia* would be absurd and it remains to consider its position in relation to the other genera of the Pygopodidae. It shares with *Pygopus*, *Paradelma*, *Delma* and *Lialis* a unique character, a pair of post-cloacal bones forming external hooks *as a secondary sex character of the male.* These structures were first described and figured in 1870 by Fürbringer in *Lialis* (*burtoni*) but without the realization that they were associated with sex ; the same author also described the limbs and girdles of *Pygopus*, but found no such structures because, presumably, his specimen was a female. Boulenger (1885 : 239) mentioned, as a family character, the presence of a spur laterally behind the vent, but wrongly described it as a projection of the ischium and did not, apparently, observe that it was only present in the one sex. Kinghorn (1923 : 134), alone, seems to have observed that in *Aprasia* the spurs are present in males only. The present writer has confirmed that they are, likewise, secondary sex characters of the male in the other four genera mentioned above.

Post-cloacal bones occur in male geckoes (Smith, 1933 : 9), a fact taken into consideration, with others, by McDowell & Bogert in aligning the Pygopodinae and Lialinae with the Gekkota ; but it seems unlikely that development of these bones to form external hooks would have occurred twice in Australasia, and nowhere else, *pari passu* with reduction of limbs, the acquisition of a serpentiform habit and sundry other features. So the position of *Aprasia* in the Pygopodidae seems assured. Within this family it is unique in its reduced dentition, degenerate eye, absent tympanum, rudimentary middle ear (Shute & Bellairs, 1953), the lack of a splenial bone (McDowell & Bogert, fig. 21) and vestigial shoulder girdle ; the latter is much more complete in both *Pygopus* and *Lialis* (Fürbringer, 1870 : pl. i, figs. 5, 6 : Kinghorn, 1926). It differs from *Lialis* in its paired parietal bones and resembles *Pygopus*, *Paradelma*, *Delma* and *Pletholax* in this respect. If, therefore, subdivision of the Pygopodidae into subfamilies is desirable, there would be justification for placing *Aprasia* in a distinct subfamily by itself. This procedure would, however, tend to obscure the fact that the genera *Pygopus*, *Paradelma*, *Delma* and *Aprasia* form an almost continuous linear series showing progressive limb-reduction and shortening and consolidation of the skull. *Aprasia* is the most completely " degenerate " of the series as it is also, probably, the most truly fossorial.

SPECIES, RACES AND VARIATION

As already mentioned, the material examined is divisible into five morphological groups which form a rational geographical picture, briefly as follows :

I. A postocular shield present.
  (*a*) Snout prominent (fig. 3A), 1·5 to 2·1 times as long as the eye.[1] A suture normally runs from the nostril to the second labial, the nasal and second labial shields being in contact.
    (1) Presacral vertebrae 95–110 (mean 101·4). Mid-body scale rows 12 or 14. Victoria, South Australia, Nurina (W.A.).
    (1) *Aprasia striolata striolata.*
    (2) Presacral vertebrae 88–94 (mean 91·8). Mid-body scale rows 12. Albany, Plantagent and Tambellup (W.A.).
    (2) *Aprasia striolata glauerti.*

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[1] The method of measurement is important and is discussed below (p. 375).

(*b*) Snout less prominent (Text-figs. 3B and 6), 1·1 to 1·8 times as long as the eye. No suture running from the nostril. Presacral vertebrae 98–110 (mean 98·5) in males and 102–105 (mean 103·5) in females. Mid-body scale rows 14. Albany to Geraldton (W.A.): ? Northern Territory.

(3) *Aprasia pulchella.*

II. No postocular shield. Snout very prominent, 1·4 to 2·5 times as long as the eye (Text-figs. 3C and 7). A suture from the nostril reaches the prefrontal so that the nasal and second labial shields are not in contact or meet at a point only.

(*a*) Presacral vertebrae 96–112 (mean 102·8) in males and 98–116 (mean 108) in females. Mid-body scale rows 12 (rarely 14). Albany to Shark Bay (W.A.).

(4) *Aprasia repens repens.*

(*b*) Presacral vertebrae 125, male and 137, female. Mid-body scale rows 14. Hermite Island (W.A.).

(5) *Aprasia repens rostrata.*

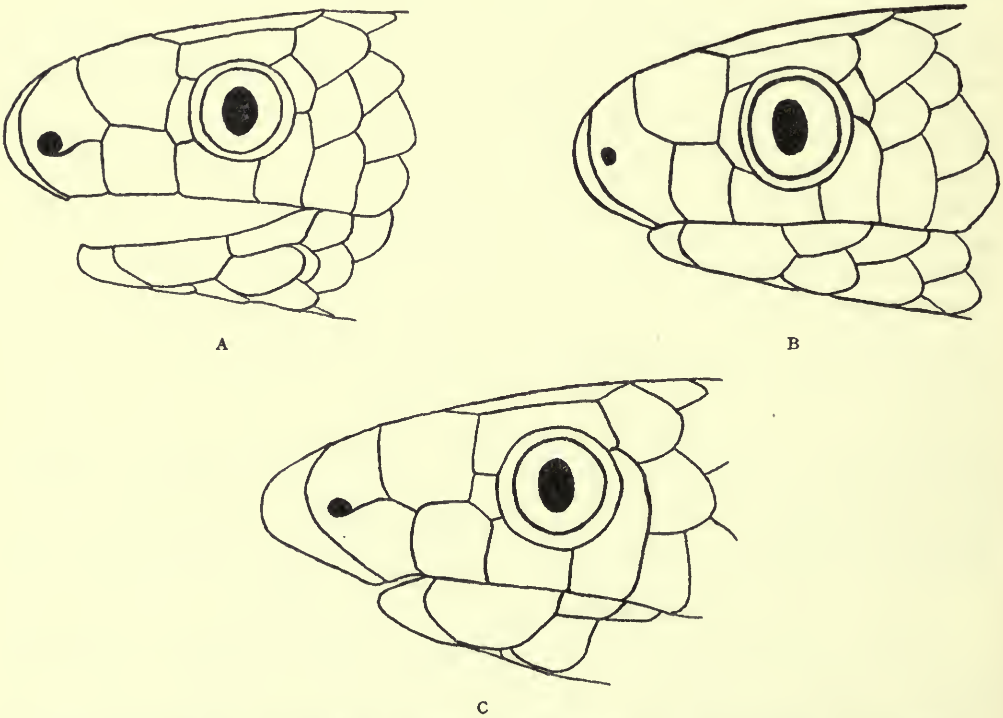

FIG. 3. Three male specimens of *Aprasia* from Albany, to show lateral head scales and proportions. A. *Aprasia striolata glauerti* subsp. nov. Holotype. B. *Aprasia pulchella* Gray. Perth Mus. 10955. C. *Aprasia repens repens* (Fry). Perth Mus. 10953.

In this synopsis the assemblages have been given specific or subspecific status and justification of these treatments is called for. It will be observed that many of the characters used in the key "break down" if they are considered without reference to geographical distribution. For instance, mid-body scale rows and numbers of presacral vertebrae show a total range of variation which permits of no absolute differentiation between what are labelled as " species ", thus :

	A. striolata.	*A. pulchella.*	*A. repens.*
Scale rows	12– 14	14	12– 14
Vertebrae	88–110	98–110	96–137

If, however, these characters are considered only in the geographical region where the three are sympatric, i.e. the Plantagenet Division of Western Australia, they provide in combination a clear cut differentiation, thus :

	A. striolata.	*A. pulchella.*	*A. repens.*
Scale rows	12	14	12
Vertebrae	88–94	98–103	96–106

A. pulchella is, additionally, completely differentiated from both of the others by its much less prominent snout with its less extensive rostral (less than one-third the diameter of the eye), the complete fusion of the nostril and first upper labial, and a distinctive colour pattern. Additional differences between *A. striolata glauerti* and *A. repens repens* exist in the same three features, viz. : Eye/rostral ratio 1·5–1·9 in *glauerti* vice 1·2–1·7 in *repens*, the suture behind the nostril running to the second labial in *glauerti* but to the prefrontal in *repens* and in colour. They are also completely differentiated by the post-ocular condition. Thus, the *Aprasias* of the Plantagenet Division can be subdivided into three different and distinct morphological groups which are not associated with age, sex, season, etc. It is reasonable to suppose that this fact signifies that there are three non-interbreeding assemblages and the only logical taxonomic treatment is to regard them as three distinct species. The most distinct morphologically is *A. pulchella* and this is also the species with the smallest geographical range (from Albany to Geraldton) and with the least variability. *A. repens* and *A. striolata* resemble each other more than either does *A. pulchella* and both show geographical variation of the same nature.

A. repens ranges northwards from Albany to the Monte Bello Islands and its distribution along this range may prove to be continuous, though the samples examined are not. The list of specimens examined, on pp. 382–383, is arranged in approximately south-north order, and it will be observed that, when due allowance is made for sexual and individual variation, there is a progressive increase in the number of presacral vertebrae from south to north ; there is also an increase in the number of mid-body scale rows from 12 to 14. It is, however, clear that the variation is not exactly correlated with latitude. For instance, in a series of sixteen males from Perth and its environs the vertebral range is from 95 to 108, whereas in a series from around Northam in almost the same latitude the range is noticeably higher, from 108 to 112. This and similar discrepancies may be due to chance and the short series available, but it seems at least equally possible that some environmental, possibly climatic, factor is involved. Although there is an overall increase in temperature from south to north, the isotherms do not follow an east–west course ;

Northam has a more "continental" climate than Perth with higher temperatures in summer, when the isotherms are locally almost parallel with the coast (c.f. *Year Book of Australia*, **40**, 1954, p. 33). Rainfall, too, though generally decreasing with decreasing latitude, also diminishes with distance from the coast. Unfortunately climatological information is not available for many of the localities from which specimens have been examined, and in any event the series are often very short. But if localities are grouped into regions around climatological stations it is possible to test, roughly, for correlation. The following table shows such groupings in relation to the six stations named. No climatic data being available for the Monte Bello Islands, the temperature and rainfall figures of Onslow have been used.

Station.	Vertebrae.		Scales.	Rainfall (annual average) (in.).	Temperature (mean December) (° F.).
	♂.	♀.			
Albany	96·0 (2)	—	12	39·7	64·2
Katanning	97·3 (3)	104·4 (8)	12	19·4	68·3
Collie	—	103·0 (2)	12	39·6	68·1
Perth	102·6 (20)	108·6 (25)	12	36·0	71·0
Geraldton	107·0 (2)	112·0 (1)	12/14	18·6	72·7
York	110·7 (3)	111·0 (2)	12	18·0	73·5
Hermite Is.	125·0 (1)	137·0 (1)	14	—	—
(Onslow)	—	—	—	9·4	83.0

There is no obvious correlation between numbers of vertebrae and rainfall, either annual or monthly. But Text-fig. 4, in which vertebrae are plotted against the mean normal temperature for December, shows a correlation very clearly, though what its significance may be remains to be discovered. It is, however, difficult not to suspect that the correlation may be due to direct cause and effect, since it has been shown experimentally that the numbers of meristic structures in poikilothermic animals may be changed by varying the temperature during development. Wade Fox (1948), for example, has shown that in a Garter Snake, the numbers of mid-body scale rows, and ventral and subcaudal scutes are higher in groups of individuals whose mothers were kept at higher temperatures during pregnancy. It has also been established that in fishes (e.g. Tåning, 1952, Lindsey, 1954) an increased temperature during the appropriate embryonic period will, in some species, result in an increased number of vertebrae, fin rays, etc. (and vice versa) within certain limits; a decrease in temperature below a certain point may also, sometimes, result in an increase of the meristic characters. Detailed information regarding the breeding season of *Aprasia* in all areas, together with temperature records of the egg sites will be necessary to establish that we are, in fact, dealing here with a thermoplastic effect. In the meantime all that can be said is that there is evidence of a cline correlated with the temperature in summer, a time of year when breeding may be expected to occur. There is a discontinuity in the series and it is, therefore, legitimate to subdivide it at the discontinuity, treating the two parts as subspecies.

A. striolata, as already mentioned, also shows geographical variation in vertebral and mid-body scale numbers. It ranges from the south of Western Australia,

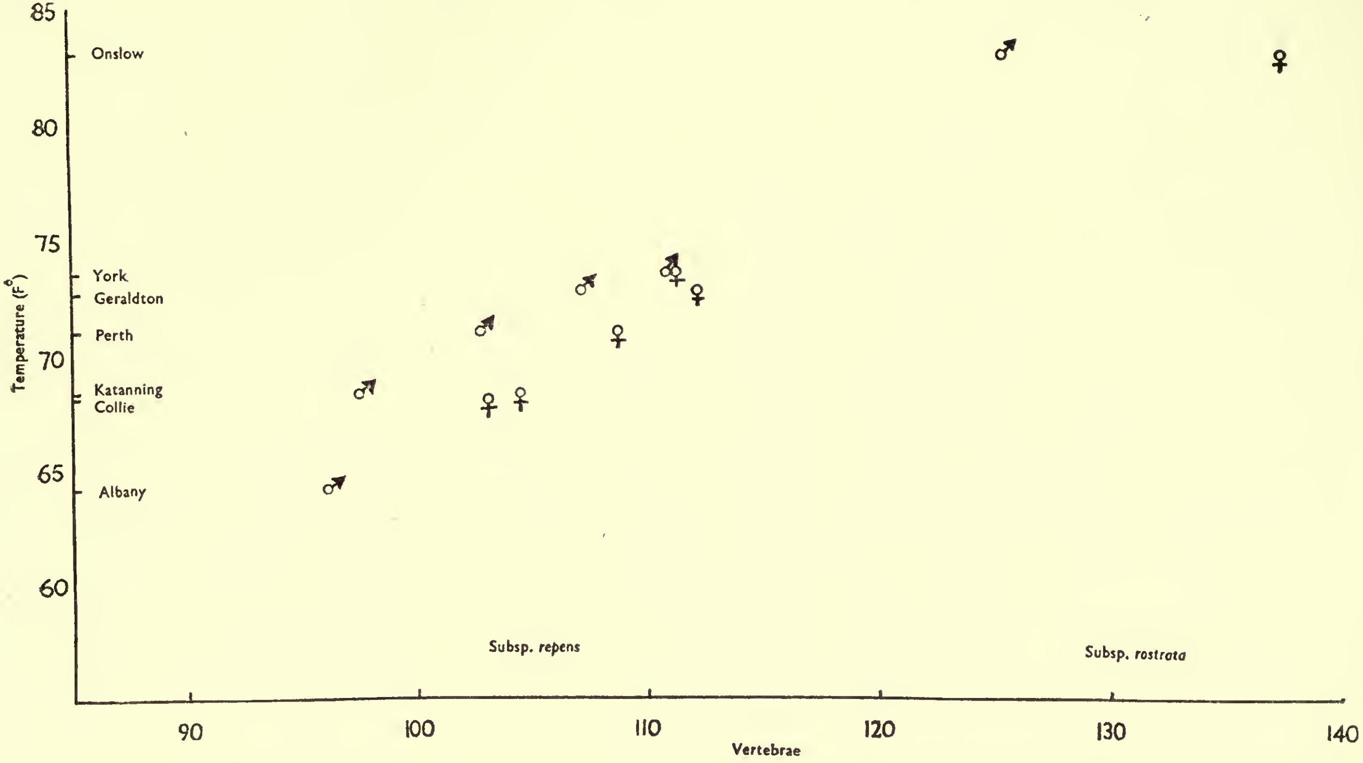

FIG. 4. *Aprasia repens.* Average numbers of presacral vertebrae in samples from areas around the climatological stations named, plotted against mean December temperatures.

where it is sympatric with *A. repens* in Albany, Plantagenet and Tambellup, across the south of the continent to western Victoria. In the west its vertebrae range from 88 to 94, there being no significant secondary sex difference, and the mid-body scales are constantly 12. In South Australia and Victoria the vertebrae range from 95 to 110 and 25% of the specimens seen have 14 scale rows. Again, as in *A. repens*, there appears to be some correlation with temperature, but not with rainfall, thus:

Station.	Vertebrae.	Scales.	Rainfall (annual average) (in.).	Temperature (mean, December) (° F.).
Albany	92·0 (11)	12	39·7	64·2
Katanning	91·3 (3)	12	19·4	68·3
Eyre (Nurina)	101·0	14	11·6	67.0
Wudinna[1]	99·0	14	15·0	71.0
Adelaide	101·4 (10)	12 or 14	21·0	70·7

[1] Climatic data estimated as intermediate between Port Lincoln and Port Augusta.

There is, however, inadequate information to establish the existence of temperature plasticity and, moreover, a marked discontinuity becomes obvious when the series is plotted (Text-fig. 5). So in the present state of knowledge the recognition of two subspecies is indicated.

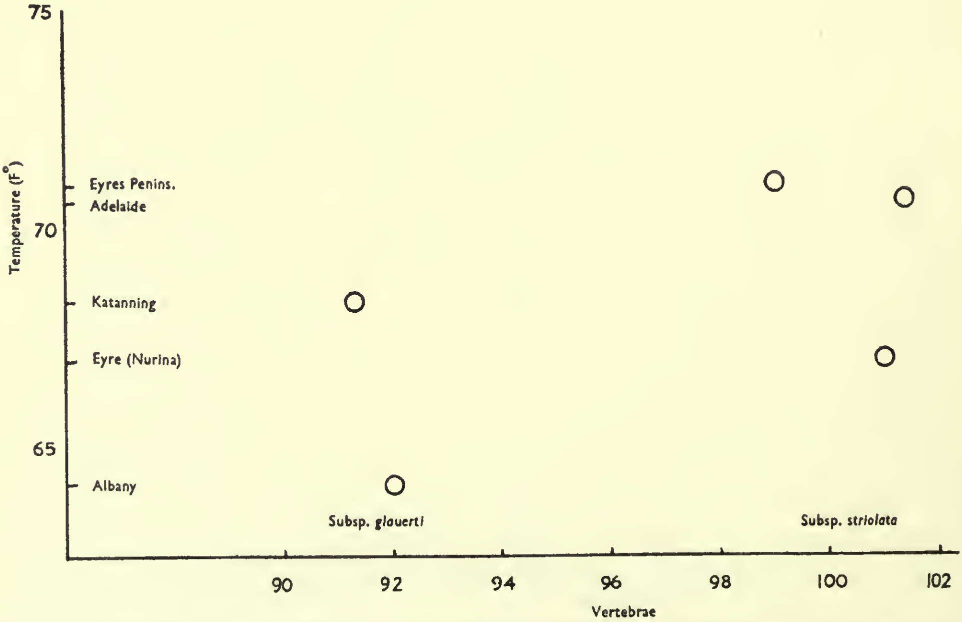

FIG. 5. *Aprasia striolata.* Average numbers of presacral vertebrae of local populations plotted against the mean December temperatures of the areas.

Only sixteen specimens of *A. pulchella* with definite localities have been examined, all from points between Albany and Geraldton. Within this restricted area there appears to be little variation ; all the specimens have 14 scale-rows and the presacral vertebrae range between 96 and 98 in males (8) and from 102 to 105 in females (8). The type, a female without precise locality, has 104. The species may have a greater geographical range and there may be some geographical or temperature variation ; one specimen seen (Sydney, No. 12529) is an immature male with a much higher number of vertebrae, 110. This specimen has no locality recorded against it in the registers of the Australian Museum, but formed part of a mixed collection mainly from the Northern Territory (Yirrikala Mission) and the northern parts of Western Australia.

The number of scales longitudinally is associated with the number of vertebrae and consequently shows the same geographical variation within each species. There are, however, differences between the species in regard to the number of scales in relation to the number of vertebrae, i.e. relative size of the scales, and the differences appear to be significant. The ratio of the number of ventral scales to the number of vertebrae varies as follows :

A. pulchella	(18)	1·44 to 1·59.	Mean	1·52 σ 0·049.
A. striolata	(28)	1·31 to 1·50.	,,	1·43 σ 0·048.
A. repens	(48)	1·23 to 1·52.	,,	1·35 σ 0·06.

Comparing the three on the criterion of the quotient of the difference of the means divided by the standard error of the difference of the means, the differences are all significant, thus :

(*a*) *A. pulchella*/*A. striolata* $\frac{d}{\sigma d} = 6{\cdot}4.$
(*b*) *A. striolata*/*A. repens* ,, $= 6{\cdot}5.$
(*c*) *A. pulchella*/*A. repens* ,, $= 11{\cdot}6.$

A. striolata is almost exactly intermediate between the other two, *A. pulchella* having the smallest scales. Increase in scale-size is often accompanied by complete or partial elimination of some scales. In *Aprasia* this effect is manifest in the head region. In *A. repens*, with the largest scales, the post-ocular has been eliminated and the pre-ocular is much reduced in size compared with the other two species (c.f. Text-figs. 3, 6 and 7). No variation in this character has been observed.

The character of length of snout relative to size of eye can be appreciated by inspection, but is difficult to measure accurately. The method adopted was to measure the distance between the tip of the rostral and the anterior corner of the frontal as seen in plan projection on a plane parallel with that passing through the tip of the rostral and the centres of the eyes, using a camera lucida for the purpose. The eye diameter is that of the brill measured horizontally, i.e. excluding the ring of small scales that borders the " window ". The method cannot be claimed to give a high degree of accuracy, but it does provide directly comparable figures although the range of variation will almost certainly be exaggerated. Comparison between the subspecies shows no significant differences, thus :

$$\left.\begin{array}{lll}\text{(a) } \textit{A. striolata striolata} \text{ (11).} & \text{Mean } 1{\cdot}67 & \sigma\ 0{\cdot}14 \\ \quad\ \textit{A. striolata glauerti} \text{ (14).} & \text{,, } 1{\cdot}78 & \sigma\ 0{\cdot}16\end{array}\right\} \frac{d}{\sigma d} = 1{\cdot}62.$$

$$\left.\begin{array}{lll}\text{(b) } \textit{A. repens repens} \text{ (65).} & \text{,, } 1{\cdot}96 & \sigma\ 0{\cdot}20 \\ \quad\ \textit{A. repens rostrata} \text{ (2).} & \text{,, } 2{\cdot}1 & ?\end{array}\right\} \frac{d}{\sigma d} = < 1.$$

Between species, however, the differences are marked and significant, thus :

A. pulchella (17). Mean 1·45 σ 0·15.
A. striolata (25). ,, 1·74 ,, 0·16.
A. repens (67). ,, 1·96 ,, 0·20.

(a) *A. pulchella/A. striolata* $\frac{d}{\sigma d}$ = 6·0.
(b) *A. striolata/A. repens* ,, = 5·5.
(c) *A. pulchella/A. repens* ,, = 11·9.

The character of the length of the rostral shield, as might be expected, is correlated with the length of the snout ; it shows no infraspecific variation that is certainly significant. As between species, however, the ratio of brill diameter to length of rostral* is :

A. pulchella (17). Mean 3·90 σ 0·53.
A. striolata (25). ,, 1·80 σ 0·14.
A. repens (65). ,, 1·52 σ 0·18.

Comparing the differences of the means for significance :

(a) *A. pulchella/A. striolata* $\frac{d}{\sigma d}$ = 16·2.
(b) *A. striolata/A. repens* ,, = 8·8.
(c) *A. pulchella/A. repens* ,, = 19·0.

Thus, it seems to be established that infra-specific variation occurs mainly, if not exclusively, in meristic characters—the numbers of vertebrae and scales. Non-meristic characters such as the length of the snout relative to the eye (and the associated character of the relative proportions of the rostral shield), the presence or absence of a post-ocular shield, and relative scale size are significantly different between the samples that are believed to represent bio-species, but show no significant geographical variation within these groups.

SYNONYMIES AND DESCRIPTIONS

Aprasia striolata striolata Lütken

Aprasia pulchella var. *striolata* Lütken, 1863, *Vidensk. Medd. Kbh.* **1862** : 300, pls. 1–2, figs. 3–3*c*.
Aprasia pulchella var. *lineolata* Lütken, 1863, loc. cit.
Aprasia octolineata Peters, 1864, *Monatsber. Ak. Berlin*, **1863** : 233.
Aprasia pulchella, Günther, 1873 *Ann. Mag. nat. Hist.* (4) **12** : 145 (part). Günther, 1875, *Zool.*

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* (Measured in plan projection.)

Erebus and Terror, **2** : 10 (part). Boulenger, 1885, *Cat. Lizards Brit. Mus.* **1** : 246 (part). McCoy, 1888, *Prodrom. Zool. Victoria*, **17** : 233, pl. 161, fig. 1. Lucas & Frost, 1894, *Proc. roy. Soc. Vict.*, N.S., **5** : 340. Lucas & le Souëf, 1909, *The Animals of Australia* (Melbourne) : 219 (part). Werner, 1912, *Das Tierreich*, **33** : 25 (part), fig. 5. Zietz, 1920, *Rec. S. Aust. Mus.* **1** : 193 (part). Kinghorn, 1923, *Rec. Aust. Mus.* **14**, 2 : 130 (part), figs. 7–9. Kinghorn, 1926, *Rec. Aust. Mus.* **15** : 63, fig. 18. Kershaw, 1927, *Vict. Nat.* **43** : 341. Waite, 1929, *Rept. and Amph. of South Australia* (Adelaide) : 95, figs. 69, 70

Ophiopsiseps nasutus (*non* Bocage), Jensen, 1901, *Vidensk. Medd. Kbh.* **1900** : 317, pl. 3.

Ophioseps nasutus, (*non* Bocage), Fry, 1914, *Rec. W. Aust. Mus.* **1** : 181 (part). Kinghorn, 1923, *Rec. Aust. Mus.* **14**, 2 : 128 (part), figs. 4–6. Kinghorn, 1926, op. cit., **15** : 62, fig. 17.

Snout projecting and rounded, its length 1·5 to 2·0 times as long as the horizontal diameter of the brill (mean 1·67, σ 0·14). Rostral well visible from above, its length contained 1·8 to 2·0 times in the length of the brill (mean 1·90, σ 0·07). A suture normally connects the nostril with the suture between the first and second labials so that the nasal and the second labial are in contact; in one specimen only of the fifteen examined are these two shields separated. A small postocular separates the fourth labial from the supraocular. Premaxillary teeth may be present, though small, in females; they are constantly present, and much larger, in males. Scales in 12 (80%) or 14 (20%) longitudinal rows at mid-body; from 140 to 155 scales, approximately, in a straight line from the mental shield to the vent in the proportion of 1·38 to 1·50 (mean 1·43, $\sigma = 0{\cdot}034$, n. 13) per vertebra. Presacral vertebrae number 98 to 104 in males (5 counted) and 95 to 110 in the nine females. A well defined colour pattern of dark lines or rows of dots is usually present on the back. The largest female examined measures 133 mm. from snout to vent and the largest male 107 mm.

This subspecies appears to range from western Victoria westwards to the Nurina Division of Western Australia. The reasons for its recognition have been discussed above. The material examined includes the immature specimens which Jensen misidentified as *Ophioseps nasutus* Bocage. The variation in the more important taxonomic characters is as follows:

Museum No.	Locality.	Sex.	Length.	Scales.	Vertebrae.	Snout. / Eye	Eye / Rostral.
Cop. R.50.2	Hochkirk, Vict.	?	57	12	100	1·7	1·8
Sydney 11759	Jeparit, Vict.	♀	?	12	?	?	?
,, 11760	,, ,,	♀	?	12	95	?	?
B.M. 1902.7.30.8	Renmark, S.A.	♀	79	12	102	1·5	1·9
,, 1902.5.30.10	,, ,,	♀	110	14	109	1·7	1·9
,, 1902.5.30.11	,, ,,	♀	109	14	101	2·0	1·8
,, 1902.5.30.12	,, ,,	♂	100	12	98	1·5	2·0
,, 1902.5.30.13	,, ,,	♂	95	12	101	1·7	2·0
,, 1862.7.19.4	S. Australia	♂	102	12	104	1·6	1·9
,, 1862.7.19.5	,, ,,	♀	118.	12	104	1·6	1·9
,, 1862.7.19.6	,, ,,	♂	110	12	100	?	?
Sydney 14382	Wudinna, S.A.	♂	107	14	99	?	?
,, 3466	?	♀	115	12	102	1·7	1·9
B.M. 46.5.2.14	?	♀	133	12	110	1·6	1·9
Perth R.5280	Eyre, Nurina, W.A.	♀	113	14	101	1·8	1·8

Aprasia striolata glauerti subsp. nov.

(Text-fig. 3A)

Snout projecting and rounded (Text-fig. 3A), its length 1·6 to 2·1 times as long as the horizontal diameter of the brill (mean 1·78, $\sigma = 0{\cdot}16$). The rostral is well visible from above, its length being contained 1·5 to 1·9 times in the length of the brill, the mean being 1·70 and σ 0·14. The condition of the nasal suture is similar to that of the eastern race, but two specimens of the fifteen are asymmetrical and have the nasal separated from the second labial on one side; in one specimen the suture is incomplete and fails to reach either the interlabial or the naso-prefrontal suture. Mid-body scale rows are constantly 12 and there are from about 120 to 140 from the mental shield to the vent in the proportion of 1·31 to 1·49 (mean 1·43, σ 0·058, n. 15) per vertebra. Presacral vertebrae number 88 to 93 in males (7) and 91 to 94 in females (8). Premaxillary teeth present in both sexes, but smaller and sometimes absent in females. Straw coloured above and beneath, sometimes with obscure darker markings suggesting dusky lines on the back. The largest male measures 109 mm. from snout to vent and the largest female 115 mm.

The type series is from the "road districts" of Albany, Plantagenet and Tambellup, as listed below, the first mentioned being the holotype.

Museum No.	Locality.	Sex.	Length.	Vertebrae.	Snout / Eye	Eye / Rostral.
Perth 10949	Albany	♂	79	93	1·9	1·6
,, 6782	,,	♀	89	92	1·7	1·5
,, 6782	,,	♂	89	88	1·6	1·8
,, 6782	,,	♀	89	91	1·9	1·7
,, 6782	,,	♀	95	94	1·9	1·5
,, 6782	,,	♂	97	93	1·8	1·9
,, 6782	,,	♀	98	93	1·7	1·8
,, 10950	,,	♀	115	92	2·1	1·6
,, 10951	,,	♀	92	91	1·9	1·6
B.M. 1911.12.18.3	,,	♀	108	93	1·7	1·7
Perth 7214	Narrikup	♂	84	93	2·0	1·9
Sydney 12305	Tambellup	♂	79	90	1·6	1·9
,, 12305	,,	♂	88	92	1·6	1·8
,, 12305	,,	♀	92	92	1·6	1·9
,, 3468	[" Australia "]	♂	109	92	?	?

Aprasia pulchella Gray

(Text-figs. 3B and 6)

Aprasia pulchella Gray, 1839, *Ann. Nat. Hist.* **2** : 332. Gray, 1841, in Grey, *Travels in Australia*, **2** : 428, 438, pl. 4, fig. 2. Gray, 1845, *Cat. Lizards Brit. Mus.* : 68 (part). Günther, 1873, *Ann. Mag. nat. Hist.* (4) **12** : 145 (part). Günther, 1875, *Zool. Erebus & Terror*, **2** : 10 (part). Boulenger, 1885, *Cat. Lizards Brit. Mus.* **1** : 246 (part). Lucas & le Souëf, 1909, *The Animals of Australia*, (Melbourne) : 219 (part). Zietz, 1920, *Rec. S. Aust. Mus.* **1** : 193 (part). Kinghorn, 1923, *Rec. Aust. Mus.* **14**, 2 : 130 (part). Kinghorn, 1926, *Rec. Aust. Mus.* **15** : 63 (part). Loveridge, 1934, *Bull. Mus. comp. Zool. Harv.* **77** : 316.

Ophioseps nasutus Bocage, 1873, *J. Sci. math. phys. nat. Lisboa*, **4** : 232. Werner, 1912, *Das Tierreich* : **33** : 25. Fry, 1914, *Rec. W. Aust. Mus.* **1** : 181 (part). Kinghorn, 1923, *Rec. Aust. Mus.* **14**, 2, 128 (part).

Ophiopsiseps nasutus, Boulenger, 1887, *Cat. Lizards Brit. Mus.* **3** : 436.

Aprasia brevirostris Werner, 1909, in Michaelsen & Hartmeyer, *Die Fauna südwest-Austral.* **2**, 16 : 266, fig. 2.

Snout slightly prominent and bluntly rounded (Text-figs. 3B and 6), its length 1·1 to 1·8 times the length of the brill (mean 1·45, σ 0·15). The portion of the rostral visible from above is less extensive than in any other species, its length being contained 3·1 to 5·0 times in the brillar length (mean 3·90, σ 0·53). No suture between the nasal and first labial shield, though in the holotype there is a vestige on the nasoprefrontal suture (Text-fig. 6). A postocular separates the fourth upper labial from the supraocular. Mid-body scale rows 14 ; from 145 to 170 scales, approximately, on the mid-line between the mental shield and the vent in the proportion of 1·44 to 1·59 (mean 1·52, σ 0·049 ; n. 18) per vertebra. Presacral vertebrae 96 to 110 in males (9) and 102 to 105 in females (9) ; the possibility of geographical variation in this character has already been discussed. Premaxillary teeth absent in females. Pale brown above with indefinite dusky linear markings on the dorsal scales which can produce a lineolate appearance ; on the head the dark markings are more irregular and produce a vermiculate appearance. The largest male examined measures 108 mm. from snout to vent and the largest female 124 mm.

This species is known with certainty to occur from Albany to Geraldton.

Although Boulenger (1885) lists two specimens as " types " of *A. pulchella*, there is nothing in Gray's original description to indicate that he had more than one specimen whose dimensions are given as 2¾ in. from snout to vent with a tail of 1¾ in. Only one of Boulenger's specimens, the one listed below as B.M. 1946.8.30.93,

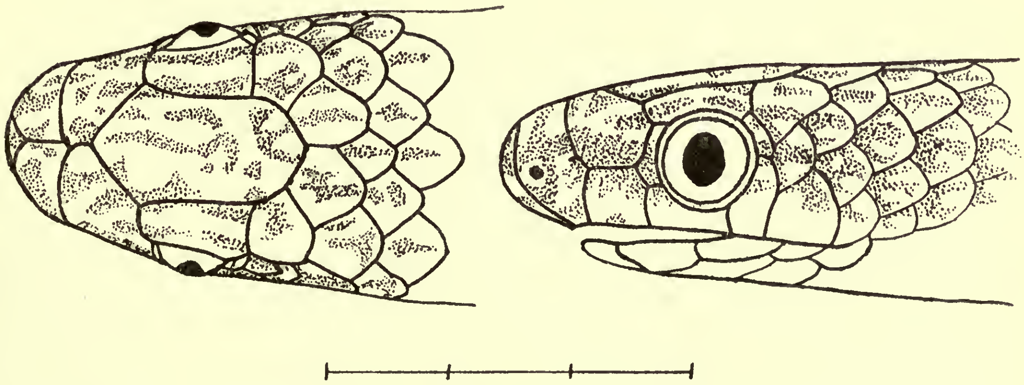

FIG. 6. *Aprasia pulchella* Gray. Holotype female.

approximates to these dimensions (snout to vent 2·8 in., tail 1·75 in.) and has vermiculate head-markings (c.f. Text-fig. 6) as figured by Gray in 1841. The only doubts on the matter arise from the facts that (1) the original description states that the nostril lies " in the suture between the top of the first labial and anterior frontal plate " and (2) Günther in 1873 stated that all the specimens then in the British Museum had only 12 mid-body scales. In the specimen now regarded as the type the first labial is fused with the shield above it and there are 14 scale rows. Günther was patently in error, as was Boulenger (1885), also, when he failed to detect more than 12 scale rows and it seems likely that Gray, using only a hand lens, was misled by the vestige of a suture.

Thanks to the courtesy of Professor Jorge the holotype of *Ophioseps nasutus* Bocage has been examined and compared with the other specimens listed. Unfortunately the specimen is in very poor condition ; it is in four fragments, breaks occurring after the ninth vertebra, in front of the nineteenth presacral, and immediately behind the pelvic girdle ; the tail tip is also wanting and the scales of the upper surface of the head are very badly abraded, so that their limits can only be determined with difficulty and a little uncertainty. It is also likely that the specimen has been partially desiccated at some time, since the cranium was full of air and the whole specimen measures only 73% of its pristine length (head and body fragments 95 vice 133 mm. and tail 38 vice 52 mm.).[1] Nevertheless, despite these defects, a sufficient number of characters can be deciphered or measured to make it virtually certain that the species involved is the same one which Gray had previously named *Aprasia pulchella*. Thus, for comparison with the characters of the species :

	O. nasutus (Type).	*Aprasia pulchella.*
Suture from nostril . .	Absent .	Absent
Snout length/brill diam. .	1·42 .	Mean 1·45
Brill diam./rostral length .	3·7 .	,, 3·9
Postocular . . .	Present	Present
Mid-body scales . .	14 .	14
Scales/vertebrae . .	1·57 .	Mean 1·52

As noted above, the skull is visible dorsally and the ratio of frontal to nasal length (1·56) is similar to that in an example of *A. pulchella* (1·50). The presacral vertebrae number 89, but it is certain that a number have been lost from the ends of most of the fragments (one was found loose) and no significance can be attached to the number. The sex cannot be determined since, although no post-cloacal bones are present, there is a clear indication of the loss of at least 4 anterior caudal vertebrae. The first of the tail vertebrae has a well-defined fracture-plane through its centrum and so cannot be one of the most anterior caudal vertebrae which possess no such split (Pratt : 184) ; in the numerous X-ray photographs of *Aprasia* that have been examined the fracture-plane is not evident anterior to the fifth to seventh caudal.

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[1] The reduction cannot be due to the loss of a single large fragment of 52 mm. because when the tail and the head-plus-body are considered separately each is shorter than originally in the same proportion.

The specimens examined and their characters are :

Museum No.	Locality.	Sex.	Length.	Vertebrae.	Snout./Eye	Eye/Rostral.
Perth 10954	Albany	♀	117	102	1·6	3·2
,, 10955	,,	♂	92	98	1·6	3·8
,, 2371	Mt. Baker	♀	109	103	1·4	3·1
,, 10711	Boddington	♂	95	96	1·5	5·0
,, 10712	,,	♂	108	97	1·6	4·0
,, 642	Wagin	♀	114	104	1·4	4·2
,, 3873	Lowden	♂	74	96	1·5	3·3
,, 1984	Mt. Helena	♀	?	104	1·8	3·6
,, 5994	Statham	♂	99	98	1·5	4·0
,, 4629	Huntley	♂	86	97	1·4	4·5
,, 3342	Darlington	♀	106	105	1·4	4·0
,, 4629A	Guildford	♀	104	103	1·4	3·5
M.C.Z. 24460	Mundaring Weir	♂	—	98	1·3	—
Perth 3409	Upper Swan River	♀	124	105	1·5	3·8
B.M. —	Swan River	♀	106	?	1·1	3·6
M.C.Z. 24467	Geraldton	♀	—	103	1·6	—
,, 24468	,,	♂	—	98	1·5	—
B.M. 1946.8.30.93	W. Australia	♀	72	104	1·2	3·5
Sydney 6553	?	?	115	?	1·4	4.7
,, 12529	?	♂	62	110	1·4	4·5
Mus. Bocage	" Australia "	?	95+	89+	1·42	3·7

Aprasia repens repens (Fry)

(Text-fig. 3C)

Aprasia pulchella (part), Gray, 1845, *Cat. Lizards Brit. Mus.* : 68. Günther, 1875, *Ann. Mag. nat. Hist.* (4) **12** : 145. Günther, 1875, *Zool. Erebus & Terror*, **2** : 10. Boulenger, 1885, *Cat. Lizards Brit. Mus.* **1** : 246. Werner, 1909, in Michaelsen & Hartmeyer, *Die Fauna südwest Austral.* **2**, 16 : 266. Lucas & le Souëf, 1909, *The Animals of Australia* (Melbourne) : 219. Werner, 1912, *Das Tierreich*, **33** : 25. Zietz, 1920, *Rec. S. Aust. Mus.* **1** : 193.

Ophioseps repens Fry, 1912, *Rec. W. Aust. Mus.* **1** : 178, fig.

Aprasia repens, Kinghorn, 1923, *Rec. Aust. Mus.* **14**, 2 : 132, figs. 10–12. Kinghorn, 1926, *Rec. Aust. Mus.* **15** : 64. Loveridge, 1934, *Bull. Mus. comp. Zool. Harv.* **77** : 317.

Lialis repens, Kinghorn, 1926. tom. cit. fig. 19.

Snout strongly projecting (Text-fig. 3C), its length 1·4 to 2·5 times as long as the brill (mean 1·96, σ 0·20). Rostral well visible from above, its length contained 1·0 to 2·4 times in the brillar diameter (mean 1·52, σ 0·18). A suture connects the nostril with the anterior border of the prefrontal so that the first labial and the prefrontal are in contact ; in two specimens the four shields (nasal, prefrontal, first labial, second labial) meet at a point and in another example the two sides are not symmetrical the nasal being in contact with the second labial on the right side but separated from it on the left. There is no postocular, the fourth labial reaching the supraocular. Premaxillary teeth absent in females. Scales in 12 (75 specimens) or 14 (1 specimen) rows at mid-body and between 125 and 165, approximately in a median line from the mental shield to the vent in the proportion of 1·23 to 1·52 (mean 1·35 ; σ 0·06 ; n. 46) per vertebra. Presacral vertebrae

96–112 in males and 98–116 in females, there being geographical, possibly temperature correlated, variation as discussed above. The ground colour is pale straw, above and below, often with ill-defined dark longitudinal lines or rows of dots on the back and especially on the flanks; head sometimes with dark markings; upper lip and throat chrome yellow; tail red or yellow. The largest male examined is 150 mm. from snout to vent and the largest female 165 mm.

The subspecies ranges from Albany to Victoria (W.A.) and possibly further north. Werner (1909) records a specimen in the Perth Museum as from Shark Bay, but there is no present record of such a specimen. The only possibility is specimen R.11360, a male which bears a label "M & H" (= Michaelsen and Hartmeyer); but Werner's record is not listed as having been obtained at any of the stations where Michaelsen and Hartmeyer worked and which are all numbered. In addition its vertebral count (104) is much more compatible with an origin near Perth.

The material examined contained these specimens:

Museum No.	Locality.	Sex.	Length.	Vertebrae.	Scales.	Snout. / Eye.
Perth 10952	Albany	♂	73	96	12	1·8
,, 10953	,,	♂	98	96	12	2·1
B.M. 1931.7.1.139	Mt. Toolbrunup	♂	95	96	12	1·7
Perth 2868	Tambellup	♀	104	104	12	1·7
,, 2869	,,	♂	83	99	12	1·9
,, 2870	,,	♀	93	103	12	1·9
,, 2871	,,	♀	95	103	12	1·8
,, 2872	,,	♀	95	104	12	1·8
,, 10692	Borden	♀	116	106	12	1·8
,, 433A	Dumbleyung	♂	82	97	12	2·1
,, 433B	,,	♀	103	105	12	2·1
,, 373	,,	♀	105	106	12	2·3
Sydney 8015	,,	♀	101	104	12	?
Perth 10246	Williams	♀	107	108	12	2·0
,, 10322	Bunbury	♀	95	98	12	1·9
,, 10895	West Midland	♂	82	101	12	2·1
,, 10894	,, ,,	♀	90	107	12	1·9
,, 10893	,, ,,	♀	82	111	12	1·8
,, 4173	Midland	♀	93	107	12	2·1
,, 766	Midland Junction	♀	107	110	12	2·0
,, 3734	Rottnest Isld.	♂	62	107	12	2·3
,, 3759	,, ,,	♂	?	92	12	2·1
,, 3765	,, ,,	♀	63	111	12	1·9
,, 4582	,, ,,	♀	109	113	12	2·3
M.C.Z. 33027	,, ,,	♂	—	110	12	—
,, 33028	,, ,,	♀	—	113	12	—
,, 33029	,, ,,	♀	—	109	12	—
,, 33031	,, ,,	♀	—	110	12	—
,, 33032	,, ,,	♀	—	110	12	—

Museum No.	Locality	Sex.	Length.	Vertebrae.	Scales.	Snout. / Eye
Perth 4373	East Perth	♂	107	105	12	2·0
B.M. 69.5.25.18	Perth	♂	100	?	12	2·3
Perth 3347	,,	♂	96	105	12	2·0
,, 2596	,,	♂	87	101	12	1·9
,, 1742	,,	♀	104	106	12	2·1
,, 6944	,,	♂	76	103	12	2·0
,, 631	,,	♀	52	?	12	2·0
,, 2251	,,	♀	98	105	12	1·9
Perth 9664	Rivervale	♂	88	101	12	2·3
,, 9665	,,	♂	55	103	12	?
,, 2837	Gooseberry Hill	♀	87	114	12	2·1
,, 8745	,, ,,	♀	110	114	12	1·7
,, 8185	Claremont	♂	78	100	12	2·0
,, 9093	Nedlands	♂	80	102	12	2·0
,, 9094	,,	♂	71	102	12	1·7
,, 5344	,,	♀	58	104	12	2·0
,, 123	Cottesloe	♂	105	106	12	2·1
,, 7405	Applecross	♂	80	95	12	2·2
,, 7406	,,	♀	72	104	12	1·8
,, 7390	,,	♂	68	99	12	2·1
,, 5310	Bayswater	♂	92	108	12	2·1
,, 8721	,,	♀	98	108	12	1·8
,, 10208	,,	♀	102	108	12	2·0
,, 2150*	Bassendean	♀	103	107	12	2.0
,, 1374	Leederville	♀	102	113	12	2·0
,, 5351	Maylands	♀	71	109	12	2·0
,, 2397	Mt. Lawley	♂	82	106	12	1·7
,, 4186	,, ,,	♂	57	101	12	1·5
,, 707	E. Freemantle	♀	47	102	12	1·4
,, 4383	,, ,,	♀	106	106	12	1·7
M.C.Z. 24427	Balcatta Beach	♂	—	105	12	—
Perth 4356	Stoneville	♀	102	108	12	1·9
,, 4357	,,	♀	63	?	12	1·6
Sydney 9138	Mundaring	♀	75	106	12	2·1
Perth 5492	Northam	♀	123	116	12	2·0
,, 8891	,,	♂	92	112	12	1·6
,, 4913	,,	♂	102	112	12	1·9
,, 6927	Bakers Hill	♂	93	108	12	2·0
,, 9222	Lomos	♀	80	106	12	2·0
,, 1730	Newmarracarra (Vict.)	?	?	?	12	2·2
,, 5064	Eradu (Vict.)	♂	60	109	14	2.5
M.C.Z. 24458	Geraldton	♀	—	112	12	—
,, 24459	,,	♂	—	105	12	—
B.M. 43.5.19.86	W. Australia	♂	85	?	12	2·0
Perth 11360	?	♂	60	104	12	2·0

* This specimen is ovigerous.

Aprasia repens rostrata subsp. nov.

(Text-fig. 7)

Aprasia sp. Hill, 1955, *Proc. Linn., Lond.* **165**, 2 : 115.

Holotype a male, collected 17.viii.52 on Hermite Island and allotype a female collected on the same island 22.v.52.

Snout very strongly projecting (Text-fig. 7) its length 2·0 times and 2·2 times as long as the diameter of the brill in male and female respectively. Rostral shield drawn out posteriorly so that the length of the portion visible from above is contained 0·9 (♂) and 0·8 (♀) times in the brillar length. The suture running backwards from the nostril meets the suture between the first and second labials in such a position that these two labials, the nasal and the prefrontal meet at a point. No post-ocular shield, the supraocular produced ventrally to make contact with the fourth labial. Premaxilliary teeth present in the male but absent in the female. Scales in 14 longitudinal rows at mid-body. Scales on the mid-line between the mental shield and the vent are about 175 in the male and 190 in the female, counted to the nearest five. Presacral vertebrae 125 in the male and 137 in the female.

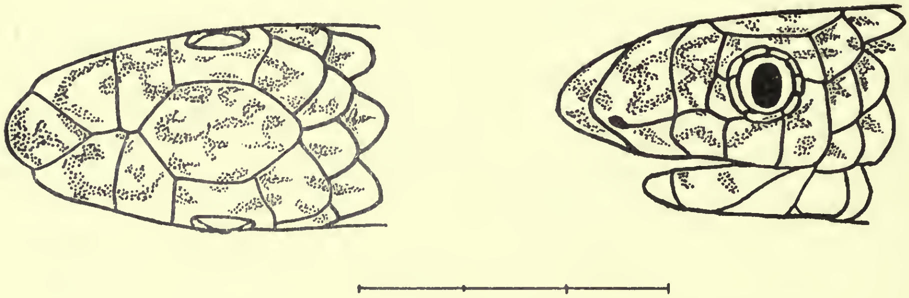

FIG. 7. *Aprasia repens rostrata* subsp. nov. Allotype female.

Pale brown above and white beneath. A broad darker lateral band on the sides of the neck which breaks up posteriorly into three fine brown lines. Three additional fine brown lines on the nape, but the mid-dorsal region of the body not lined; a single mid-dorsal dark line along the tail. Another brown line on each side of the belly. Head vermiculate.

Dimensions :

♂. Snout to vent 99 mm. ; tail 65 mm. (incomplete).
♀. ,, ,, ,, 109 mm. ; ,, 13 mm. (,,).

ACKNOWLEDGMENTS

Thanks are due to Sir William Penney who, despite his many preoccupations with the major objects of the expedition to the Monte Bello Islands, arranged for collections of the fauna and flora of the islands to be made, and to Surgeon Commander G. Wedd, R.N., who organized and supervised these activities. The resulting material touched off the present investigation, but no progress could have been made without the assistance of Mr. L. Glauert, Mr. J. R. Kinghorn, Mr. F. W. Braestrup and Mr. A. Loveridge, who have been most generous in lending comparative material from their museums at Perth, Sydney, Copenhagen and Harvard. The author is also grateful to his colleagues Mr. N. B. Marshall, and Mr. D. W. Tucker, for help with ichthyological references, and to Mr. P. E. Purves for the large number of X-ray photographs that had to be taken.

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IN THE CENTRAL HIGHLANDS OF NEW GUINEA
1950-1951

R. W. SIMS

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
ZOOLOGY Vol. 3 No. 10
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Pp. 387–438 ; *Plates* 13–14 ; 2 *Text-figures*

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BIRDS COLLECTED BY MR. F. SHAW-MAYER
IN THE CENTRAL HIGHLANDS OF NEW GUINEA
1950-1951

By R. W. SIMS

(with Field Notes and Photographs by W. T. Loke)

(Received 13th July, 1955)

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SYNOPSIS

This is a report on the birds collected by Mr. F. Shaw-Mayer in the Central Highlands of New Guinea, mainly in 1950 and 1951. Two-hundred and seventy-two specimens were obtained in the Wahgi region, principally on Mount Giluwe. Eighty-eight species and races are represented of which one race was new to science.

INTRODUCTION

1. *General*

Mr. F. Shaw-Mayer has lived and collected for many years in New Guinea and has travelled widely in the eastern half of the country. In recent years he has travelled mainly in the Central Highlands and a collection of birds from that area forms the subject of this report.

The Central Highlands of New Guinea were almost inaccessible prior to 1945 and little was known of the region, its inhabitants or its fauna. In recent years, however, the establishment of an airfield at Nondugl has made it more accessible and advantage has been taken of this for making collections by others besides Mr. Shaw-Mayer. In 1950, and again in 1952, Mr. E. T. Gilliard of the American Museum of Natural History made large collections of birds in the Wahgi region ; and during the intervening year, 1951, Count Gyldenstolpe also visited the area. The reports on these expeditions were in the course of preparation when I started identifying and making notes on Mr. Shaw-Mayer's specimens. The appearance of the first (Mayr and Gilliard, 1954) greatly facilitated the completion of these notes. The facts recorded below and the taxonomic conclusions arrived at differ for the most part only in points of detail, such as ranges of dimensions and various minor aspects of plumage colour, differences which one would expect to find in two sets of random samples from the same area. There are, however, a number of additional facts some of which suggest slight modification to Mayr and Gilliard's conclusions. These notes had been completed when I learnt that Count Gyldenstolpe's report was in the press. When it was published (Gyldenstolpe, 1955) I read it in conjunction with my own notes and referred to many specimens again. Generally there was a large measure of agreement but on one or two points our conclusions were not identical, mainly because of differences in age or sex of the specimens, or as a result of making comparisons with material from different areas.

Mr. Shaw-Mayer gave brief field notes on some specimens and a number of these are quoted here. Additional important field notes were made by Mr. Loke Wan Tho of Singapore. Mr. Loke joined Mr. Shaw-Mayer during September and October, 1952, when they travelled together up the Wahgi valley from Nondugl to Tomba. There Mr. Loke compiled most of his field notes which he kindly sent to me ; and extracts from most of them are included here. Two of his photographs are also published with his kind permission.

I wish to acknowledge the generous co-operation of the authorities in the museums at Berlin, Harvard, Leiden, New York and Pittsburgh. They have very kindly lent me specimens for examination or made critical notes on specimens sent to them for comparison. I would also like to acknowledge the help afforded to me by Mr. R. P. Derek Goodwin. He made a preliminary examination of the Shaw-Mayer Collection and I found his notes most useful. Finally I wish to thank Mr. J. D. Macdonald for reading the manuscript and for his helpful criticism.

2. *Methods*

The report of the American Museum of Natural History Expeditions (Mayr and Gilliard, 1954) contained descriptions of the topography and ecology of the area, and lists of the birds typical of the various habitats and their zoogeographical affinities. These subjects, therefore, receive no further treatment in this report except where new information is presented.

The sequence of the families, genera and species and the nomenclature are that of Mayr (1941*b*). In that work a synonymy of each name is given and consequently only the original reference to each name is normally given here.

The specimens are listed under their British Museum (Natural History) register numbers together with information provided by the collector. The dimensions are given in millimetres ; the wings were flattened when they were measured so the measurement given is the arc ; the bill measurement is that of the exposed part of the culmen.

3. *Summary of New Information*

(*a*) Additions to the list of the birds of the Wahgi region (Gyldenstolpe, 1955).

Casaurius bennetti shawmayeri.[1]
Dupetor flavicollis gouldi.
Falco peregrinus ernsti.
Porzana pusilla palustris.
Alcyone azurea ochrogaster.
Cisticola exilis diminuta.
Petroica bivittata bivittata.
Aplonis metallica metallica.
Neositta papuensis alba.[2]

(*b*) Zoogeographical affinities of Wahgi region birds not listed by Mayr and Gilliard, 1954.

Southern affinities (Australia) :
Porzana pusilla palustris

Cisticola exilis diminuta

North-eastern affinities (Huon Peninsula) :
Turnix maculosa giluwensis

Western affinities (Mountains of Dutch New Guinea) :
Neositta papuensis alba

South-eastern affinities :
Casuarius bennetti shawmayeri (Krätke Mountains)
Circus spilonotus spilothorax
Petroica bivittata bivittata

Northern affinities (Sepik Region) :
Alcyone azurea ochrogaster
Astrapia stephaniae femina

(*c*) Habitats of Wahgi region birds not listed by Mayr and Gilliard, 1954.

Grasslands—4,000 ft. to 7,500 ft.

Dupetor flavicollis gouldi
Anas superciliosa rogersi
Circus spilonotus spilothorax
Turnix maculosa giluwensis
Alcyone azurea ochrogaster
Cisticola exilis diminuta

Mid-mountain forest—7,500 ft. to 9,000 ft.

Casuarius bennetti shawmayeri
Scolopax saturata rosenbergii
Aplonis metallica metallica
Astrapia stephaniae femina
Neositta papuensis alba

Timber-line, edge of the alpine grasslands—11,000 ft.
Petroica bivittata bivittata

COLLECTING LOCALITIES

October, 1946 : Menebe, Mount Hagen, 5,000 ft.
October, 1950 : Headwaters of the Minj River, Kubor Range, 8,000 to 9,000 ft.
November, 1950 ; Minj, Wahgi River, 5000 ft. ; and the forested slopes of the Kubor Range.
December, 1950 and January, 1951 ; Forested ridges on the west slopes of the Hagen Range near Welya, 7,500 ft. to 10,000 ft.

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[1] Racial identity problematical, Gyldenstolpe (1955).

[2] Possibly includes *Neositta papuensis wahgiensis* Gyldenstolpe, 1955.

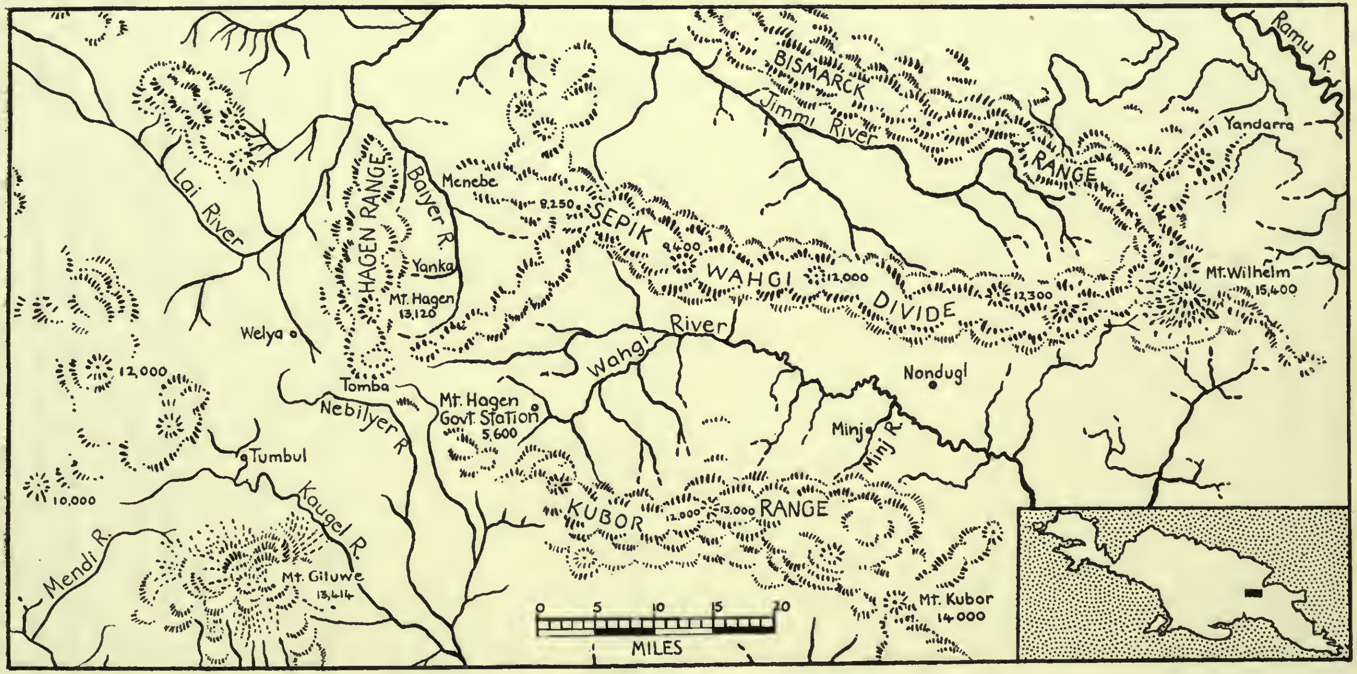
Ramu R.
Yandarra
BISMARCK
Jimmi River
RANGE
Mt. Wilhelm
15,400
12,300
DIVIDE
WAHGI
12,000
SEPIK
9,400
8,250
Menebe
Baiyer R.
HAGEN RANGE
Yanka
Mt. Hagen
13,120
Lai River
Welya
Tomba
Nebilyer R.
Mt. Hagen
Govt. Station
5,600
Wahgi
River
Nondugl
Minj
Minj R.
KUBOR
12,000
13,000
RANGE
Mt. Kubor
14,000
12,000
10,000
Tumbul
Kaugel R.
Mt. Giluwe
13,414
Mendi R.
0
5
10
15
20
MILES

FIG. 1.—Map of the Wahgi region, Central Highlands, New Guinea.

February and March, 1951 : South slopes of the Hagen Range near Tomba, 8,000 to 10,000 ft.

March to July, 1951 : Plateau grasslands north of Mount Giluwe, 7,300 ft. Lamende Range north-west of Mount Giluwe, 8,500 ft. (23rd March). Moss Forest, 10,000 ft.; and the alpine grasslands, 11,000 ft.; Mount Giluwe (24–28th April).

Moss Forest, 10,000 ft.; and the alpine grasslands, 11,000 feet, Lamende Range (11th to 14th May).

Forested north slopes, 7,500 to 8,500 ft.; and the mid-mountain grasslands, 9,000 ft., Mount Giluwe (20th to 30th May).

Mount Giluwe rises to 13,414 ft. above sea-level from a grassland plateau of 7,300 ft.. The lower slopes of the mountain are forested up to about 9,000 ft. where the mid-mountain grasslands commence. These are separated from the alpine grasslands of the summit by the moss forest that extends approximately from 10,000 ft. to 11,000 ft.. The distribution of the forests and grasslands appears to be similar on the Lamende Range and characteristic of the mountains of this area ; fuller details, particularly of the Bismarck, Hagen and Kubor Ranges, were given by Mayr and Gilliard (1954 : 323).

ANNOTATED LIST OF BIRDS COLLECTED IN THE WAHGI REGION BY MR. F. SHAW-MAYER

Casaurius bennetti shawmayeri Rothschild

Casuarius papuanus shawmayeri Rothschild, 1937, Bull. Brit. Orn. Club, **57**, p. 120. Arau district, Krätke Mountains, New Guinea.

1954.17.266 ; 1 ♀; Menebe, north of Mount Hagen, 5,000 ft.; October, 1946.

MEASUREMENTS. 1 ♀—height of back from ground, 860 ; total length, 1,170. COLOURS : bill and casque, shiny black ; legs, horn ; iris, brown. STOMACH CONTENTS : remains of hard fruits.

The specimen and a drawing of the head and neck at death agree with the type. The record extends the known range of *shawmayeri* about 150 miles north-west from the Krätke Mountains to the Hagen Range. It is probable that this race is found throughout the Wahgi Valley area, but it remains to be seen how far it extends into the mountains on each side. Mr. Gilliard saw a cassowary on Mount O'-Mar in the Kubor range which he believed was this race (Mayr and Gilliard, 1954 : 331), and the present specimen taken near Mount Hagen supports his provisional identification.

Dupetor flavicollis gouldi (Bonaparte)

Ardetta gouldi Bonaparte, 1855, Consp. Gen. Av. **2**, p. 132. New South Wales, Australia.

1953.17.1 ; 1 ♂ ; Mount Giluwe, 7,300 ft.; June, 1951.

MEASUREMENTS : 1 ♂—wing, 209 ; tail, 76 ; bill, 69. COLOURS ; bill, upper mandible dark horn and lower mandible light horn ; legs, brown-grey ; iris, yellow. STOMACH CONTENTS : water insects.

Anas superciliosa rogersi Mathews

Anas superciliosa rogersi Mathews, 1912, Austr. Av. Rec. **1**, p. 33. Augusta, south-western Australia.

1953.17.2–4 ; 1 ♂, 2 juv. ♂ ; Mount Giluwe, 7,300 ft.; June, July, 1951.

MEASUREMENTS : 2 juv. ♂—wing, 229, 239 ; tail, 68, 71 ; bill 46, 48. 1 ♂—wing 250 ; tail 96 ; bill 47. COLOURS : bill, slate (ad. ♂ black at base of lower mandible) ; legs, pale brown flesh (ad. ♂ greenish pale brown, darker on webs of feet) ; iris, brown. STOMACH CONTENTS : insect larvae, grass seeds and river gravel.

These birds were taken on the plateau north of Mount Giluwe where the species was plentiful. The June birds appear to be juveniles because the feathers of the undersurface have a dark brown streak unlike the adult, where they are dark brown and fringed with cinnamon. The primaries are fully grown and show no signs of wear, yet the wing is shorter than the adult's. In this respect the young birds approach the smaller size of the other New Guinea race, *pelewensis*, which differs from *rogersi* only in the shorter wing—*pelewensis*, 230 ; *rogersi*, 250—Amadon (1945 : 3) ; nevertheless, this pair appear to be young birds of the larger form, *rogersi*. I have not seen any material of comparable age and plumage, but it is likely that the primaries of the juvenile plumage which persist throughout the first adult plumage are shorter than the primaries of the full adult plumage. The young birds have started to moult and a few adult patterned feathers have come in on the undersurface ; the wing does not appear to be involved in the moult. The July bird, taken nearly six weeks later, is completing moult. The feathers of the undersurface of all three specimens are variably stained a rust colour, probably with iron oxide.

Salvadorina waigiuensis Rothschild and Hartert

Salvadorina waigiuensis Rothschild and Hartet, 1894, Novit. Zool. **1**, p. 683. ? Waigeu, possibly Vogelkop, north western New Guinea.

1953.17.5–6 ; 2 ♀ ; Mount Giluwe, 7,300–7,200 ft.; April, July, 1951.

MEASUREMENTS : 2 ♀—wing, 180–185 ; tail, 95 ; bill, 34–35. COLOURS : bill, dull yellow with black along the centre of the upper mandible ; legs, yellowish horn (webs of feet almost black) ; iris, dark brown. STOMACH CONTENTS : river gravel, water beetles and other small aquatic insects.

Accipiter melanochlamys schistacinus (Rothschild and Hartert)

Astur melanochlamys schistacinus Rothschild and Hartert, 1913, Novit. Zool. **20**, p. 482. Mt. Goliath, Oranje range, central New Guinea.

1953.17.7–8 ; 1 ♂, 1 ♀ ; Mount Giluwe ; 8,000 ft.; May, July, 1951.

MEASUREMENTS : 1 ♂—wing, 216 ; tail, 160 ; bill, 15·5. 1 ♀—wing, 251 ; tail, 184 ; bill, 18. COLOURS : bill, black (cere—♂ yellow and ♀ orange-yellow) ; legs,

♂ bright yellow and ♀ orange ; claws, black ; iris, ♂ bright yellow and ♀ bright orange. STOMACH CONTENTS : ♂, remains of small bird ; ♀, remains of frog.

The female (July) is in moult and the new black feathers of the back have a greenish metallic lustre in contrast to the worn feathers which have faded to a rusty brown-black. The male (May) is a young bird in fresh immature plumage. The exposed parts of the feathers of the back are chestnut in colour edged with rufous brown, the unexposed parts being white. The feathers of the shoulders and most of the head are white tipped with black, while the crown is chestnut in colour. The primaries and the retrices are dark brown with black-brown barring above ; they are silvery below with irregular cinnamon coloured areas, particularly on the inner webs. The feathers of the under-surface are cream in colour with a median chestnut stripe while those of the legs are more buffy with a narrow rufous stripe.

Circus spilonotus spilothorax Salvadori and D'Albertis

Circus spilothorax Salvadori and D'Albertis, 1875, Ann. Mus. Civ. Genova, **7**, p. 807. Yule Island, south-eastern New Guinea.

1953.17.9 ; 1 ♂ ; Mount Giluwe, 7,300 ft.; July, 1954.

MEASUREMENTS : 1 ♂—wing, 375 ; tail, 220 ; bill, 21·5. COLOURS : bill, black (cere, bluish horn ; dorsal surface, greenish yellow.) ; legs, dull yellow ; claws, black ; iris, bright yellow ; inside of mouth, blue-grey.

" I often observed this fine bird soaring over the grasslands of the plateau, sometimes high in the air, at other times a few feet above the grass. Several times it came to rest on the ground, but it was not observed to be eating anything. At the approach of the hunter it was off, sailing with speed in ever widening circles. Once noticed at dusk, but more often during the early morning. It appeared to be alone." (F. S.-M.).

In comparison with other birds of this race this specimen is considerably darker in colour, both above and below. The upper-parts are a rusty black and lack the typical silvery white wash which is present only over the upperside of all except the inner and outer pairs of rectrices. The inner rectrices are almost black above and the outer a faded chestnut colour, none being spotted like those of other specimens. This bird exhibits a type of melanism not uncommon among birds of prey, but it appears to be darker than any reported by Rand (1941*a* : 1).

Falco peregrinus ernesti Sharpe

Falco ernesti Sharpe, 1894, Ibis, Ser. 6, **4** : 545. Mt. Dulit, Sarawak.

1953.17.10.; 1 ♂ ; Mount Giluwe, 7,3000 ft.; July, 1951.

MEASUREMENTS : 1 ♂—wing, 292 ; tail, 144 ; bill, 19. COLOURS : bill, dark horn around cere and gape, base of mandible yellow ; legs, yellow (claws, black) ; iris, black (skin around eye, yellow).

Aepypodius arfakianus (Salvadori)

Talegallus arfakianus Salvadori, 1877, Ann. Mus. Civ. Genova, **9** : 333. Arfak Mountains, north-western New Guinea.

1953.17.11–12 ; 1 ♂, 1 ♀ ; Mount Giluwe, 9,000 ft.; April, July, 1951.

MEASUREMENTS : 1 ♂—wing, 278 ; tail, 132 ; bill, 31. 1 ♀—wing, 272 ; tail, 145 ; bill, 30. COLOURS : bill, yellowish-green-horn ; legs, greenish-yellow (♀, frontal scutes, dark horn) ; iris, greenish yellow ; head, pale bluish white, reddish colouring along top of gape from back of beak to below eye (♂, purple comb and wattles, bluish area on crown to hinder end of the base of the comb ; ♀, two small pinkish wattles—no comb—bluish area above wattles). STOMACH CONTENTS : pieces of hard fruits.

The birds were taken in the forest on the north slopes of Mount Giluwe. An egg was found in the oviduct of the female (July).

Synoicus ypsilophorus lamonti Mayr and Gilliard

Synoicus ypsilophorus lamonti Mayr and Gilliard, 1951, Amer. Mus. Novit. No. **1524**, p. 1. Tomba Central Highlands, New Guinea.

1953.17.13–24 ; 7 ♂, 5 ♀ ; Mount Giluwe, 7,500–7,200 ft.; April, May, 1951.

MEASUREMENTS : 7 ♂ : wing, 90–100 ; bill, 12–13·5. 5 ♀—wing, 93–98 ; bill, 12–13. COLOURS ; bill, black, bluish horn at base ; legs, greenish yellow ; iris, yellow-orange. STOMACH CONTENTS : chiefly grass seeds, some insects and gravel.

Most of the specimens of this fine series match closely 2 ♂ and 2 ♀ of the race *lamonti* taken by Mr. Gilliard at Tomba, which is only a few miles north of Mount Giluwe. The exception is the male bird (No. 1953.17.19) taken on 27th May. In general colour it is a much paler brown, more heavily barred above and below and the white shaft streaks of the feathers of the back are wider and more pronounced. It was sent to the American Museum of Natural History where, in Mr. Gilliard's absence, Dr. Amadon kindly compared it with other material of *S. ypsilophorus*. He found that it was unlike any other bird of this species and that the differences between this specimen and other examples of *lamonti* are greater than those between *lamonti* and neighbouring races. As these races appear to be fairly stable in their characteristics we have concluded that this specimen is probably aberrant.

" This quail was plentiful on the grasslands at 7,000 feet, and on the grasslands on the north slopes of Mount Giluwe up to 8,000 feet. Sometimes a single bird would flush, at other times three or more. Much of the country is peaty, almost swampy, and these conditions seem to suit it best " (F. S.-M.).

FIELD NOTES. Six of these quail were started up in pairs from the long grass near Nondugl. A roughly made nest of grass was found on the ground among the weeds near some land under cultivation on 15th September. The nest contained four buff-coloured eggs with thickly distributed minute brown spots.

Excalfactoria chinensis subspecies ?

Tetrao chinensis Linnaeus, 1766, Syst. Nat. 12th ed., **1**, p. 277. China.

1953.17.25–33 ; 3 ♂, 6 ♀ ; Mount Giluwe, 7,500–7,200 ft.; April, May, 1951.
MEASUREMENTS : 3 ♂—wing, 65–68 ; bill, 8–9. 6 ♀—wing, 65–70 ; bill, 9–10. COLOURS : bill, black ; legs, orange, orange-yellow (2 ♀ with greenish tinge) ; iris, 3 ♂—brownish-red ; 6 ♀—dark brown. STOMACH CONTENTS : grass seeds and gravel.
The series was collected on the grasslands north of Mount Giluwe. The birds are in fresh plumage with the exception of the female taken on 7th April which is in moult although it had an egg in the oviduct. Two races of *E. chinensis* have been described from New Guinea, *papuensis* Mayr and Rand from Mafulu in the south-east and *novaeguineae* Rand from the Balim River in the Snow Mountains. Mount Giluwe is approximately midway between the type localities of these races and, as might be expected, the birds from there exhibit characteristics of both. The series was compared with specimens of both races collected by Dr. Rand. The adult males differ but little from a male taken at Lake Daviumbo on the Fly River and compared with typical *papuensis* the bluish colour of the head is slightly less pronounced and the small feathers of the head have dark grey-brown tips ; in this respect they approach the characteristics of *novaeguineae*. The adult female from Mount Giluwe differ from *papuensis* only in the colour of the under-parts, where there are gradations from the richer colour of *papuensis* to the paler colour of *novaeguineae*.

The series is almost intermediate between *papuensis* and *novaeguineae*. I am not, therefore, naming them racially. Furthermore, Dr. Rand's birds are in old plumage, whereas in most of these the plumage is fresh.

Turnix maculosa giluwensis Sims

Turnix maculosa giluwensis Sims, 1954, Bull. Brit. Orn. Club, **74**, p. 37. Mount Giluwe, Central Highlands, New Guinea (8,000 ft.).

1953.17.34–41[1] ; 1 ♂, 1 juv. ♂ ; 3 ♀, 3 juv. ♀ ; Mount Giluwe, 8,000–7,200 ft. ; May, June, 1951.
MEASUREMENTS : 2 ♂—wing, 65 ; tarsus, 18.5–19 ; bill, 10–11. 6 ♀—wing, 70–75 ; tarsus, 19–20 ; bill, 11·5–14. COLOURS : bill, yellowish, ridge and tip dark horn ; feet, yellow with greenish tinge ; iris, cream. STOMACH CONTENTS : grass seeds and small insects.
This fine series of Button-quail was taken on the open and lightly wooded grasslands around Mount Giluwe. It appears that this is the first time that such a large series of *T. maculosa* has been taken in one locality in New Guinea ; the males, particularly, are rare to collections. On examination these birds were found to be distinct enough to recognize as representatives of a new race of *T. maculosa* in

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[1] Type 1953.17.40

comparison with the other two New Guinea races, *furva* Parkes from Finschhafen on the east coast of the Huon Peninsula and *horsbrughi* from Yule Island off the south-east coast. They differ from these races by the underparts being considerably paler, but resemble *furva* by being very dark above. In size *giluwensis* is closer to *horsbrughi* than to *furva*, which is slightly larger. The one June bird is in fresh plumage the others are involved in moult.

Rallus pectoralis captus Mayr and Gilliard

Rallus pectoralis captus Mayr and Gilliard, 1951, Amer. Mus. Novit. No. **1524**, p. 2. Tomba, Central Highlands, New Guinea.

1953.17.42; 1 ♂; Hagen Range, 8,000 ft.; February, 1951.

1953.17.43–45; 1 ♂, 1 juv. ♂, 1 ♀; Mount Giluwe, 7,500–7,300 ft.; April, June, 1951.

Measurements: 3 ♂—wing, 102–104; tail, 37–40; bill, 33. 1 ♀—wing, 102; tail, 40; bill, 34. Colours: bill, dull red, dark horn near tip; legs, brownish grey; iris, yellow to brown (juv. ♂, grey brown). Stomach contents: slugs and water insects.

The adult male and female taken in February and April respectively are in worn plumage; the barring of the abdomen is faded and the flanks are stained a pinkish hue. The adult male taken in June is in fresh plumage; but the young male, also taken in June, is in full moult. In this bird the new feathers of the under-parts, unlike the worn ones, are strongly barred like those of the adults. The adult male from the Hagen Range is topotypical and both it and the other adult male show the characteristics of *captus* given by Mayr and Gilliard, but the wings average a little longer (wing, ♂ 95–102), like those of specimens taken at Nondugl by Gyldenstolpe (1955: 32). The adult female, in comparison with the adult male, has the back paler in colour by being a clearer olive-brown, less reddish. In the juvenile male the crown and the neck lack the maroon-chestnut of the adult and there is a reduction in the white barring of the back. In this respect the young bird agrees with a series of adults of *R. p. pectoralis* (Temminck) from eastern Australia.

Rallus philippensis wahgiensis Mayr and Gilliard.

Rallus philippensis wahgiensis, Mayr and Gilliard, 1951, Amer. Mus. Novit. No. **1524**, p. 3. Nondugl, Central Highlands, New Guinea.

1953.17.46; 1 ♂; Mount Giluwe; 7,500 ft.; July, 1951.

Measurements: 1 ♂—wing, 153; tail, 76; bill, 31; tarsus, 41. Colours: bill, dark horn, base of lower mandible reddish; legs, light brown; iris, reddish brown. Stomach contents: insects.

This specimen differs only in size from a topotypical male collected by Mr. Gilliard. The wing and the tail are longer and the tarsus shorter, the measurements of *wahgiensis* given by Mayr and Gilliard are : wing, 137, 140 ; tail, 62.5 ; tarsus, 44, 45. In this respect it matches specimens taken at Nondugl by Gyldenstolpe (1955 : 32).

Porzana pusilla palustris Gould

Porzana palustris Gould, 1843, Proc. Zool. Soc. Lond. **1842**, p. 139. Tasmania.

Porzana pusilla mayri Junge, 1953, Zool. Meded., Leiden, **31**, p. 247. Paniai, western New Guinea.

1953.17.47–49 ; 2 ♀, 1 juv. ♀ ; Mount Giluwe, 8,000–7,500 ft.; May, June, 1951. MEASUREMENTS : 3 ♀—wing, 79–83 ; tail, 35–40 ; bill, 14·3–15. COLOURS : bill, olive-green, tip horn colour ; legs, olive-green ; iris, orange-red. STOMACH CONTENTS : small insects.

The Mount Giluwe birds may be distinguished from a series of *palustris* from eastern Australia on very slight colour differences. The upper-parts of the New Guinea birds are somewhat warmer in tone and the under-parts a slightly clearer grey, but these differences may be attributable to the freshness of the skins. Junge (1952 : 247) was the first to report the presence of this species in New Guinea. He distinguished a new race, *mayri*, on a series from Paniai separating it from the Australian birds on a greater wing length. The measurements of the material before me, however, do not support this separation for there is some variation.

Australian birds, in B.M. (N.H.) :	Wing, 75–81	75–85
,, ,, (Junge, 1952 : 247) :	,, 80–85	
New Guinea ,, in B.M. (N.H.) :	,, 79–83	76–83
,, ,, ,, (Junge, 1952 : 247) :	,, 76–79	

Porzana tabuensis edwardi Gyldenstolpe

Porzana tabuensis edwardi Gyldenstolpe, 1955, Ark. f. Zool., Ser. 2, 8, p. 3. Nondugl, Central Highlands, New Guinea.

1953.17.50-56 ; 2 ♂, 1 juv. ♂ ; 2 ♀, 2 juv. ♀ ; Mount Giluwe, 8,000–7,5000 ft.; March, April, June, 1951.

MEASUREMENTS : 3 ♂—wing, 78–85 ; tail, 41–50 ; bill, 18–19. 4 ♀—wing, 78–80 ; tail, 41–46 ; bill, 16–18. COLOURS : bill, black ; legs, coral-red ; iris, orange-red. STOMACH CONTENTS : insects and grass seeds.

Gyldenstolpe (1955 : 34) separated the birds of the Wahgi Valley on their darker colour and slightly longer bill in comparison with a series of *tabuensis* from the Tuamoto Archipelago and Rapa Island. These characters are present in the Mount Giluwe birds and distinguish them from a series from various Pacific islands. The adult male taken in April is in worn plumage, while that taken in June is in fresh. The fresh plumage is more vinous above and more blue than slate-grey below. The young male, 31st March, differs from the adult in having the chin and throat white and the abdomen and under-wing coverts a pale whitish-grey. This bird is in moult. The adult females taken in April are starting moult with a few new feathers coming through on the back. Of the two young females one, 5th April, has nearly completed moult; while the other, 7th April, has only a few new feathers coming through on the back.

Rallicula forbesi subspecies?

Rallicula forbesi Sharpe, 1887, in Gould's "Birds of New Guinea", pt. 23, pl. (70). Owen Stanley Range, south-western New Guinea.

1953.17.57; 1 ♂; Hagen Range; 8,000 ft.; February, 1951.
1953.17.58–62; 1 ♂, 4 ♀; Mount Giluwe; 7,400–7,300 ft.; May, June, July, 1951.

MEASUREMENTS: 2 ♂—wing, 111–112; tail, 77–79; bill, 24–25. 4 ♀—wing, 108–112; tail, 63–68; bill, 24–26. COLOURS: bill, brown-black; legs, brown-black to black; iris, pale to dark brown.

The two males differ only very slightly from the type and a series of *forbesi* from south-eastern New Guinea in that the plumage is somewhat richer in tone. The four females, on the other hand, exhibit an interesting variation. Although they appear to be inseparable from the allotype and a series of *forbesi* in most respects there are differences in the speckling and the occurrence of a red-chestnut fringe on the feathers of the back. The July bird agrees with the allotype in colour and pattern in that over the back the speckling is the typical buff colour and many of the feathers are fringed imperfectly with a red-chestnut colour. Gradations are found in the other females to the colour and pattern of a May bird (1953.17.62) in which the spotting is no longer buff but white, and replaced over the scapulars by white streaks; also none of the feathers of the back have a red-chestnut fringe. The markings of this specimen so approached the description of the race *steini* which Rothschild described on one female from the Weyland Mountains that it was sent to the American Museum to be compared with the unique type. There Dr. Amadon, in Mr. Gilliard's absence, kindly examined the specimens and found that the Mount Giluwe bird matched the type. Mayr and Gilliard (1954: 335) described a similar variation in a Wahgi region series which they named *steini* mainly on the length of the tail. The present series, however, cannot be separated from the nominate form on measurement, while on plumage most of the birds approach *forbesi*. It seems that if the present series were combined with the birds reported by Mayr and Gilliard then phenotypical *forbesi* and *steini* would be present in approximately equal numbers in addition to the specimens grading between the two. In view of this I do not venture to name the birds of the present series at racial level.

One explanation of the occurrence of this variation in these series from the Wahgi region could be that the two races have come into breeding contact following a period of reproductive isolation. It seems that such an interpretation, based on the material available, would not be entirely incorrect because a population showing such a high incidence of heterogeneity would be unlikely to occur in a cline. It seems equally unlikely that the type of *steini* and other specimens that resemble it are variants for no similarly patterned birds have been reported from southeast of the Wahgi region.

Pluvialis dominca fulva (Gmelin)

Charadrius fulvus Gmelin, 1789, Syst. Nat. **1**, pt. 2, p. 687. Tahiti.

FIELD NOTE. Six of these plovers were seen together in a " paddock " at Nondugl on 15th September. A few of the black feathers of the breeding plumage could be seen on the under-surface of some of the birds.

Scolopax saturata rosenbergii Schlegel

Scolopax rosenbergii Schlegel, 1871, Ned. Tijdschr. Dierk. **4**, p. 54. Arfak Mts., north-western New Guinea.

1953.17.63–65 ; 2 ♂, 1 ♀ ; Mount Giluwe, 9,500–9,000 ft.; May, June, 1951.
1953.17.66–67 ; 1 ♂, 1 ♀ ; Lamende Range, 9,500–9,000 ft.; June, 1951.

MEASUREMENTS : 2 ♂—wing, 145–146 ; tarsus, 33–34 ; bill, 82–83. 3 ♀—wing, 148–155 ; tarsus, 32–35 ; bill, 83–87. COLOURS : bill, brown-black horn ; legs, dark brown-grey ; iris, dark brown. STOMACH CONTENTS : worms, grubs, small beetles and other insects.

" The Woodcock is a bird of the high mountain-forest on Mount Giluwe and the Lamende Range. It lives on the ground, where it searches for insects and digs for worms and grubs. During the early morning it will often rise and fly high above the trees, where it can be heard calling ; later it drops down again on to the forest floor " (F. S.-M.).

The black barring of the feathers of the back is appreciably heavier than in topotypical specimens of *rosenbergii*. In this respect the present series is similar to the specimens that I have seen from the Oranje Mountains taken by Dr. Rand who considered that this difference was of no racial significance. (1942*b* : 439). The wing measurements are less that those of Dr. Rand's specimens but Shaw-Mayer's birds are in moult and it seems that the primaries are not fully grown. In these moulting birds the brown of the new feathers is noticeably redder and darker than that of the old.

Gallicolumba beccarii beccarii (Salvadori).

Chalcophaps beccarii Salvadori, 1875, Ann. Mus. Civ. Genova, **7**, p. 974. Hatam, Arfak Mountains, north-western New Guinea.

1953.17.68 ; 1 ♂ ; Hagen Range, 8,000 ft.; March, 1951.
1953.17.69 ; 1 ♂ ; Mount Giluwe, 7,500 ft.; May, 1951.

MEASUREMENTS : 2 ad. ♂—wing, 107,109 ; tail, 60,70 ; bill, 14. COLOURS : bill, black ; legs, dark purple ; iris, brown-black. STOMACH CONTENTS : hard seeds.

Charmosyna papou goliathina Rothschild and Hartert

Charmosyna stellae goliathina Rothschild and Harter, 1911, Novit. Zool. **18** ,p. 160. Mt. Goliath, Oranje Range, central New Guinea.

1953.17.70–73; 2 ♂, 2 ♀; Mount Giluwe, 9,000-8,500 ft.; April, June, July, 1951.

MEASUREMENTS: 2 ♂—wing, 151, 155; tail, 297, 324; bill, 18. 2 ♀—wing, 150, 152; tail, 256, 280; bill, 17, 19. COLOURS: bill, orange to dark red; legs, bright orange; iris, orange-red. STOMACH CONTENTS: flowers and fruit pulp.

The two males are in the dark phase plumage. The June and July birds of both sexes are completing moult.

FIELD NOTE. Native name, " Kai-niginch ".

Oreopsittacus arfaki grandis Ogilvie-Grant

Oreopsittacus grandis Ogilvie-Grant, 1895, Bull. Brit. Orn. Club, **5**, p. 15. Owen Stanley Mountains, south-eastern New Guinea.

1953.17.74–76; 1 ♂, 2 ♀; Hagen Range, 9,500–9,000 ft.; December, 1950.

MEASUREMENTS: 1 ♂—wing, 81; tail, 84; bill, 8. 2 ♀—wing, 82, 86; tail, 85; bill, 8, 9. COLOURS: bill, black; legs, green-grey; iris, black-brown.

These birds match *grandis* except in wing length. In this respect the females are larger than both *grandis* and *major* and the males intermediate,—*grandis*: ♂, 73–76; ♀, 73—*major*: ♂, 85–87; ♀, 80—(Ogilvie-Grant, 1915: 169).

Neopsittacus musschenbroekii major Neumann

Neopsittacus musschenbroekii major Neumann, 1924, Ornith. Monatsber. **32**, p. 38. Schraderberg, Sepik Mountains, northern New Guinea.

1953.17.77; 1 ♂; Mount Giluwe, 7,500 ft.; June, 1951.

MEASUREMENTS: 1 ♂—wing, 114; tail, 101; bill, 16. COLOURS: bill, yellow; legs, brown-grey; iris, orange-red. STOMACH CONTENTS: fruits and berries.

Other birds taken in the same area were identified as *major* by Mayr and Gilliard (1954: 339) but the present example differs from other material of the species in being much darker. Compared with *major*, the crown, collar, nape and sides of the throat are browner and washed with crimson. The chin and throat are dark brown with a greenish wash. The back appears to be very dark due to the feathers being fringed with dark brown. Some of the primary wing coverts, the outer webs of the primaries and the upper surfaces of the two central rectrices are almost entirely dark brown with a slight greenish wash. The pattern of the underparts is similar to *major*, but the green is replaced by olive and the crimson by a yellowish-brown. This specimen may be an abnormally pigmented bird of the race *major*, although the possibility that it represents a distinct form should not be overlooked.

Psittacella brehmii pallida A. B. Meyer

Psittacella pallida A. B. Meyer, 1886, Zeitschr. ges. Ornith. **3**, p. 3. Astrolabe Mountains, south-eastern New Guinea.

Psittacella bürgersi Reichenow, 1918, Journ. f. Ornith. **66**, p. 244. Schraderberg, Sepik region, northern New Guinea.

Psittacella brehmi ornata Mayr, 1931, Mitt. Zool. Mus. Berlin, **17**, p. 720. Dawong, Herzog Mountains, south-eastern New Guinea.

1953.17.78–79; 1 ♂, 1 ♀; Mount Giluwe, 8,500 ft.; June, 1951.

1953.17.80–81; 1 ♂, 1 juv. ♀; Hagen Range, 9,000 ft.; February, 1951.

MEASUREMENTS: 2 ♂—wing, 122, 125; tail, 86; bill, 18, 20. 1 ♀—wing, 127; tail, 87; bill, 18. 1 juv.♀—wing, 122; tail, 86; bill, 17. COLOURS: bill, metallic blue-grey, becoming white towards tip in juvenile; legs, dark grey, green-grey in the ad. ♂; iris, orange, grey in juvenile. STOMACH CONTENTS: hard berries and seeds.

Gyldenstolpe (1955 : 57) described much of the individual variation in both coloration and size in the birds of this species from central and south-eastern New Guinea. He showed that *bürgersi* should be regarded as a synonym of *pallida* and agreed with Mayr (1941 : 69) who had previously united *ornata* with *pallida*. Of the present specimens the adult female and the juvenile were sent to the Berlin Museum, where Professor Stresemann, who kindly made the comparison, found that they closely matched the type of *P. bürgersi* Reichenow. In view of the evidence presented by Gyldenstolpe I am naming the birds of this present series *pallida*. Compared with a small series of *intermedia* from southern Dutch New Guinea the Wahgi region birds are more bluish-green above with a greenish wash over the crown; and the sides of the head are more greyish in colour.

Psittacella picta excelsa Mayr and Gilliard

Psittacella picta excelsa Mayr and Gilliard, 1951, Amer. Mus. Novit. No. **1524**, p. 6. Mount Orata, Kubor Mountains. Central Highlands, New Guinea.

1953.17.82; 1 ♂; Hagen Range, 9,000 ft.; February, 1951.

1953.17.83; 1 juv. ♂; Kubor Range, 8,000 ft.; October 1950.

1953.17.84; 1 ♂; Mount Giluwe, 11,000 ft.; April, 1951.

MEASUREMENTS: 2 ♂—wing, 114, 116; tail, 73; bill, 14, 15. 1 juv. ♂—wing, 103; tail, 68; bill, 12·5. COLOURS: bill, pale blue, yellowish (juv. ♂); legs, grey; iris, orange-yellow, grey-yellow (yg. ♂). STOMACH CONTENTS: seeds and small hard berries.

The adult from the Hagen range differs from the Mount Giluwe bird and a topotypical specimen taken by Mr. Gilliard in that the golden-yellow patches on each side of the neck are joined over the neck by a narrow band of the same colour. The young male resembles a topotypical female also collected by Mr. Gilliard.

Psittacella modesta hallstromi Mayr and Gilliard

Psittacella modesta hallstromi Mayr and Gilliard, 1951, Amer. Mus. Novit. No. **1524**, p. 5 Yandarra, north slope of Mount Wilhelm, Bismarck Mountains, New Guinea.

1953.17.85–87 ; 2 ♂, 1 ♀ ; Mount Giluwe, 8,500–8,000 ft.; April, June, 1951.
1953.17.88 ; 1 juv. ♂ ; Kubor Range, 8,000 ft.; October, 1950.
1953.17.89 ; 1 ♂ ; Hagen Range, 9,500 ft.; February, 1951.

MEASUREMENTS : 4 ♂—wing, 98–101 ; tail, 59–62 ; bill, 14. 1 ♀—wing, 102 ; tail, 64 ; bill, *damaged*. COLOURS : bill, metallic blue-grey ; legs, dark blue-grey ; iris, orange (2 ad. ♂), yellow-brown (2 imm. ♂), dark brown (1 ad. ♀). STOMACH CONTENTS : seeds and pieces of hard berries.

The young male taken in October is starting to moult from juvenile plumage in which the throat and breast are an olivaceous colour and lack the ashy-brown of the adult male. The feathers of the breast are also faintly barred with yellow as in the female where the orange and black barring of the breast merges into the plain green of the abdomen and flanks. The head and the nape are the same colour as the back although the feathers at the base of the bill are washed with blue and some on the hind neck are heavily barred with orange and black. The February bird is in worn plumage, while the April and June birds are in fresh plumage. The testes of the June male are enlarged.

Cacomantis pyrrhophanus excitus Rothschild and Hartert

Cacomantis excitus Rothschild and Hartert, 1907, Novit. Zool. **14**, p. 436. Angabunga River, south-eastern New Guinea.

1953.17.90–91 ; 1 ♂, 1 juv. ♂ ; Mount Giluwe, 7,500 ft.; April, May, 1951.

MEASUREMENTS : 1 ♂—wing, 145 ; tail, 140 ; bill, 17. 1 juv. ♂—wing, 122 ; tail, 100 ; bill, 14. COLOURS : bill, black ; legs, yellow ; iris, dark brown. STOMACH CONTENTS : caterpillars and flying insects.

These birds were taken in the wooded country on the north slopes of Mount Giluwe. The May bird is similar to a male from the Utakwa River in Dutch New Guinea except that the grey of the chin extends to the throat. The young male which is in fresh plumage (April) is plain chestnut above and rufous-brown irregularly barred with black below.

Chalcites meyerii (Salvadori)

Chrysococcyx meyerii Salvadori, 1874, Ann. Mus. Civ. Genova, **6**, p. 82. New name for *Chrysococcyx splendidus* A. B. Meyer, 1874, Sitzungsber, Akad. Wiss. Wien, **69**, p. 81. Hatam, Arfak Mountains. (NOT Gray, 1847).

1953.17.92 ; 1 ♂ ; Wahgi River ; 5,000 ft.; November, 1950.

MEASUREMENTS : 1 ♀—wing, 88 ; tail, 65 ; bill, 12·5. COLOURS : bill, black ; legs, blue-grey ; iris, dark brown.

Tyto tenebricosa arfaki (Schlegel)

Strix tenebricosa arfaki Schlegel, 1879, Notes Leyden Mus. **1**, p. 101. Arfak Mountains, north-western New Guinea.

1953.17.95; 1 ♂; Hagen Range, 8,500 ft.; March, 1951.
1953.17.96; 1 ♀; Lamende Range, 8,500 ft.; March, 1951.

MEASUREMENTS: 1 ♂—wing, 275; tail, 119; tarsus, 62. 1 ♀—wing, 292; tail, 130; tarsus, 73. COLOURS: bill, dark horn (ad. ♂, lower mandible pale horn); legs, dark flesh; iris, brown-black. STOMACH CONTENTS: 1 ♂, remains of a rat.

Tyto longimembris papuensis Hartert

Tyto longimembris papuensis Hartert, 1929, Novit. Zool. **35**, p. 103. Owgarra, Angubunga River, south-eastern New Guinea.

1953.17.93–94; 1 ♂, 1 ♀; Mount Giluwe, 7,400 ft.; May, 1951.

MEASUREMENTS: 1 ad. ♂—wing, 343; tail, 114; tarsus, 84. 1 ad. ♀—wing, 357; tail, 123; tarsus, 97. COLOURS: *not recorded.* STOMACH CONTENTS: nil.

"♂, taken from nest in tree-hollow brooding three well incubated eggs; time, 10 a.m. ♀, taken near hollow containing nest; time, 10 a.m. Usually one or two of these Grass Owls could be seen flying low over the grasslands or sitting on an old tree fern stump during the late afternoon or at dusk. The species was, however, uncommon on the plateau, possibly the altitude was a little too great for it. It was plentiful on the grasslands east of the Hagen Range at about 5,000 feet." (F. S.-M.).

It is interesting that the male was taken while brooding the eggs as it is generally accepted that it is not usual for the males of this species to share in incubation. The eggs were "well incubated" on the 26th May, so it appears that the breeding season of the New Guinea bird is similar to that of *walleri*, from Australia, which breeds during May and June. It is worth mentioning, perhaps, that in November, 1946, Mr. Shaw-Mayer collected a pair of Grass Owls at Yanka and in comparison the birds from Mount Giluwe are slightly more tawny above and none of the feathers of the back have white shaft streaks. The male from Yanka resembles the females in that the feathers of the sides of the face-ring and the chin are tipped with brown and the face is washed with the same colour, whereas these parts are white in the male from Mount Giluwe.

Ninox theomarcha theomarcha (Bonaparte)

Spiloglaux theomarcha Bonaparte, 1885, Compt. Rend. Acad. Sci. Paris, **41**, p. 654. Triton Bay, south-western New Guinea.

1953.17.97; 1 juv. ♀; Hagen Range, 8,200 ft.; February, 1951.

MEASUREMENTS: 1 juv. ♀—wing, 188; tail, 98; tarsus, 29. COLOURS: bill, dark horn; legs, pale green-flesh; iris, bright yellow. STOMACH CONTENTS: remains of large insects.

The bird has started post-juvenile moult with new feathers coming through on the breast, but towards the vent the paler juvenile plumage persists.

Podargus papuensis Quoy and Gaimard

Podargus papuensis Quoy and Gaimard, 1830, Voy. Astrolabe, Zool. **1**, p. 207 (pl. 13). Dorey, Vogelkop, north-western New Guinea.

1953.17.98 ; 1 ♀ ; Mount Giluwe, 7,300 ft.; May, 1951.

MEASUREMENTS : 1 ad. ♀—wing, 285 ; tail, 271 ; tarsus, 20. COLOURS : bill, horn ; legs, dark grey ; iris, dark orange-red. STOMACH CONTENTS : beetles.

Taken in the woodlands at the north base of Mount Giluwe.

Aegotheles albertisi salvadori Hartert

Aegotheles salvadori Hartert, 1892, Cat. Bds. Brit. Mus. **16**, p. 649. Astrolabe Mountains, south-eastern New Guinea.

1953.17.99–103 ; 2 ♂, 1 ♀, 2 juv. ♀ ; Hagen Range, 8,500 ft.; February, 1951.

1953.17.104–105 ; 1 juv. ♂, 1 juv. ♀ ; Mount Giluwe, 7,500 ft.; April, May, 1951.

MEASUREMENTS : 3 ♂—wing, 118–121 ; tail, 97–98 ; bill, 8–9. 4 ♀—wing, 116–125 ; tail, 97–102 ; bill, 8–9. COLOURS : bill, upper mandible dark horn and lower mandible pale horn ; legs, dark flesh ; iris, dark brown. STOMACH CONTENTS : insects.

Nearest to *salvadori* but like the specimens described by Mayr and Gilliard (1954 : 342) they differ from the typical form by the underparts being somewhat more coarsely marked. The younger birds are moulting, the older are mostly in worn plumage.

Aegotheles insignis insignis Salvadori

Aegotheles insignis Salvadori, 1875, Ann. Mus. Civ. Genova, **7**, p. 916. Hatam, Arfak Mountains. north-western New Guinea.

1953.17.106 ; 1 ♂ ; Mount Wilhelm, Bismark Range ; 6,000 ft.; May, 1951.

1953.17.107–111 ; 2 ♂, 1 juv. ♂, 3 ♀ ; Hagen Range, 8,500–8,000 ft.; February, March, 1951.

1953.17.112–114 ; 1 juv. ♂, 2 ♀ ; Mount Giluwe, 8,000–7,500 ft.; March, June, 1951.

MEASUREMENTS : 4 ♂—wing, 157–170 ; tail, 132–142 ; tarsus, 21–22. 5 ♀—wing, 158–177 ; tail, 135–155 ; tarsus, 21–23. COLOURS : bill, upper mandible dark brown and lower mandible pale horn ; legs, flesh ; iris, dull yellow to brown. STOMACH CONTENTS : beetles and other insects.

This series exhibits the colour phases of this race reported by Hartert (1930 : 95) and Rand (1942*b* : 456). There are three light phase and six dark phase birds, three of the latter being considerably darker than any I have seen before.

Eurostopodus archboldi (Mayr and Rand)

Lycornis archboldi Mayr and Rand, 1935, Amer. Mus. Novit. No. **814**. p. 4. Mount Tafa, Wharton Range, south-eastern New Guinea.

1953.17.119 ; 1 ♂ ; Tomba, Hagen Range, 8,000 ft.; February 1951.

1953.17.120–121 ; 2 ♀ ; Mount Giluwe, 7,500–7,300 ft.; May, June, 1951.

MEASUREMENTS : 1 ♂—wing, 120 ; tail, 156 ; bill, 9·5. 2 ♀—wing, 123, 125 ; tail, 145, 149 ; bill, 10. COLOURS : bill, black ; legs, dark grey ; iris, brown-black. STOMACH CONTENTS : insects.

The male is in worn plumage and there is little spotting on the breast because many of the feathers have lost their rufous tips. The May female is in fresh plumage and shows numerous breast spots. A further difference between these specimens seems to be due to fading for the colour of these spots is paler in the male than in the female. These differences are interesting because they are qualitatively the same but quantitatively greater than those between two specimens collected by Dr. Rand ; namely, a male taken at Lake Habbema in Dutch New Guinea and a topotypical female taken in September. These match the male and the May female respectively of the present series, even in the plumage of the male being more worn than that of the female. Rand (1942*b* : 457) suggested that the differences between these specimens might indicate that the Dutch New Guinea birds form another race, but on this point he was not certain. The evidence provided by the birds from the Central Highlands suggests that these are seasonal differences. Dr. Rand also noted a slight difference in the colour and clarity of the black markings and vermiculations of the scapulars and inner secondaries of his birds. In all the birds of the present series these tend to be closer to the Lake Habbema bird in colour and to the Mount Tafa bird in clarity, so it may well be that this small sample is from a mixed population.

Collocalia esculenta esculenta (Linnaeus)

Hirundo esculenta Linnaeus, 1758, Syst. Nat. **10**th ed., p. 191. " China " error for Ambon (*ex* Rumphius).

FIELD NOTES : These swiftlets often occurred in pairs ; once, however, about 12 were seen hawking for insects above a native clearing on a steep hillside at about 6,000 ft.. A nest was found under a bank beside a stream, in it were two elongate eggs a pale blue-white in colour (10th September). The nest was made of fine roots and thickly covered with a yellowish coloured dry lichen that hung from the trees.

Collacalia hirundinacea hirundinacea Stresemann

Collocalia fuciphaga hirundinacea Stresemann, 1914, Verh. Ornith. Ges. Bayern, **12**, p. 7. Setakwa River, Dutch New Guinea.

FIELD NOTE : A few birds were seen, two being found on the nest. The nests were built of fine rootlets, thin black stalks and a few pieces of moss with some earth towards the bottom. An elongate egg was found in one of the nests.

Alcyone azurea ochrogaster Reichenow

Alcyone ochrogaster Reichenow, 1903, Journ. f. Ornith. **51**, p.149. Ramu River, northern New Guinea.

1953.17.115 ; 1 ♀ ; Minj, Wahgi River, 5,000 ft.; November, 1950.

MEASUREMENTS : 1 ♀—wing, 77 ; tail, 33 ; bill, 46. COLOURS : bill, black ; tip pale horn ; legs, orange-red ; iris, *not recorded*. STOMACH CONTENTS : insects.

This bird matches *ochrogaster* except that the upper-parts are a duller blue like *lessonii*.

Clytoceyx rex rex Sharpe.

Clytoceyx rex Sharpe, 1880, Ann. Mag. Nat. Hist. (5) **6**, p. 231. East Cape, New Guinea.

1953.17.116 ; 1 ♀ ; Mount Wilhelm, Bismarck Range, 6,000 ft.; May, 1950.

MEASUREMENTS : 1 ♀—wing, 173 ; tail, 137 ; bill, 37. COLOURS : bill, pale horn (base of upper mandible dark horn) ; legs, green-grey ; iris, black-brown. STOMACH CONTENTS : remains of large beetles.

This bird is more richly coloured than others I have seen of the species. This is interesting because Paludan described *septentrionalis* on the paler undersurface of three specimens from the nearby Sepik area. In size it is intermediate between *rex* and *imperator* van Oort from the Noord River—*imperator*,♀ : wing, 180 ; tail, 148 ; (van Oort, 1909 : 79)—*rex*, ♀ : wing, 160–165 ; tail, 115–125.

Halcyon sancta sancta Vigors and Horsfield.

Halcyon sancta Vigors and Horsfield, 1827, Trans. Linn. Soc. London, **15** ; p. 206. New South Wales, Australia.

1953.17.117–118 ; 2 ♂ ; Mount Giluwe, 7,600–7,500 ft.; May, 1951.

MEASUREMENTS : 2 ♂—wing, 91, 92 ; tail, 59, 60 ; bill, 35, 37. COLOURS : bill, black (lower mandible pale towards base) ; legs, dark-grey ; iris, dark-brown.

These non-breeding visitors were taken in the wooded hills north of Mount Giluwe. Both are in moult.

Hirundo tahitica frontalis Quoy and Gaimard

Hirundo frontalis Quoy and Gaimard, 1830, Voy. Astrolabe, Zool. **1**, p. 204, pl. 12. Dorey, north-western New Guinea.

FIELD NOTE. About 15 to 20 of these birds were to be seen on most evenings on the earthy bank around the pond at Nondugl (8th September).

Edolisima montona montona (Meyer)

Campephaga montona A. B. Meyer, 1874, Sitzungsber. Akad. Wiss, Wein, **69**. p. 386. Arfak Mountains, north-western New Guinea.

1953.17.122 ; 1 ♂ ; Hagen Range, 8,000 ft.; March, 1951.

MEASUREMENTS : 1 ♂—wing, 135·5 ; tail, 101 ; bill, 16. COLOURS : bill, black ; legs, black ; iris, black-brown. STOMACH CONTENTS : berries.

Rothschild and Hartert (1907 : 464) examined birds of this species and found that the adult males from the mountains of western New Guinea had longer wings than those from the mountains of the south-east ; they named these shorter-winged birds *minus*. This difference in wing length, however, does not appear to be so well marked now that more material is available ; Junge (1953 : 40), for example, reported that the wing lengths of some adult males in a series from one locality in western New Guinea were within the range of measurements of *minus*. Nevertheless, until more material is available from other localities the species cannot be reviewed satisfactorily but it seems probable that when this is done *minus* will be found to be no longer a valid race separable on wing length. The specimen from the Hagen Range is similar in measurement to some of the birds reported by Junge.

Wing Length of Adult Males

Western New Guinea.		South-eastern New Guinea.	
Rothschild and Hartert .	136·5–141·5	Rothschild and Hartert . .	128–132
Junge	131 –141·5	British Museum (Natural History)	125–134

Coracina longicauda longicauda (De Vis)

Grauculus longicauda De Vis, 1890, Ann. Rep. Brit. New Guinea, **1888–89**, p. 59. Musgrave Range, south-eastern New Guinea.

FIELD NOTE. A nest was found about 50–60 ft. above the ground in a fork of a horizontal branch on a somewhat isolated tree in the forest near Tomba. It was saucer-shaped and built of fine rootlets, the outside was decorated with lichens and moss. There was one juvenile on 11 October, which was fed by both parents. The food appeared to consist mainly of winged insects, but on two occasions (13th October) lizards were brought. After being fed with the first one, which had been pushed down its throat with some difficulty, the young bird made a gurgling noise which may have been a begging call somewhat stifled by the full crop. On the second occasion when a lizard was brought to the nest only the tail protruded from the adult's mouth, the adult then regurgitated the lizard to give it to the young. When the nest was examined on the following day (14th October) an uneaten green lizard was found there. The nest was kept under observation for about three and a half hours and the feeding visits that the adults paid to the nest during that time were recorded as follows :

08.35 : Male and female.
08.37 : Female.
08.47 : Female.
09.43 : Male and Female.
10.30 : Male.
10.42 : Male.
11.25 : Male and female.
12.07 : Male.

Nest sanitation was attempted only once, but that may have been because the birds had been disturbed. When it was not being fed the young bird remained wonderfully still, it never changed its position during the whole of the morning while it was being watched from the hide. On another day the bird was moved around in its nest so that it faced the sun, it turned immediately and resumed its former position.

Anthus gutturalis rhododendri Mayr

Anthus gutturalis rhododendri Mayr, 1931, Mitt. Zool. Mus. Berlin, **17**, p. 692. Mongi-Busu, Saruwaged Mountains (2,600 m.), north-eastern New Guinea.

1953.17.123–124 ; 1 ♂, 1 juv. ♂ ; Hagen Range, 11,000 ft.; February, 1951.
1953.17.125–131 ; 4 ♂, 3 ♀ ; Mount Giluwe, 12,000–11,500 ft.; April, 1951.

MEASUREMENTS : 5 ♂[1]—wing, 98–101 ; tail, 74–79 ; bill, 12–14. 3 ♀—wing, 94–97 ; tail, 74–77 ; bill, 13–14. COLOURS : bill, black ; legs, dark horn ; iris, dark brown. STOMACH CONTENTS : grass seeds and insects.

[1] Measurements of 1953.17.124 not given owing to broken plumage.

Anthus australis exiguus Greenway

Anthus australis exiguus Greenway, 1935, Proc. New England Zool. Club, **14**, p. 35. Wau, Morobe district, north-eastern New Guinea.

1953.17.132–138 ; 3 ♂, 3 ♀, 1 juv. ♀ ; Mount Giluwe, 7,300 ft.; May, June, 1951.

MEASUREMENTS : 3 ♂—wing, 84–86 ; tail, 62 ; tarsus, 26–27 ; pollux (not claw), 9–9·5 ; claw of pollux, 10–13 ; bill, 13·5–14. 3 ♀—wing, 80–82 ; tail, 55–59 ; tarsus, 26 ; pollux (not claw), 9 ; claw of pollux, 11–13 ; bill, 12–14. 1 juv ♀—wing, 76 ; tail, 53 ; tarsus, 25 ; pollux (not claw), 9 ; claw of pollux, 12 ; bill, 13. COLOURS : bill, dark horn (lower mandible paler towards base) ; legs, dark flesh to horn ; iris, dark brown. STOMACH CONTENTS : insects.

" This pipit was plentiful on the plateau at just over 7,000 feet. It was especially numerous on any cleared area of grassland and in the native gardens. As many as 50 to 60 were observed in the early morning and late afternoon on a recently made football field near Tumbal." (F. S.-M.).

No colour difference can be seen between most of the males and females of this series and the type and allotype respectively of *exiguus* kindly sent on loan to me by Mr. Greenway, One adult male, however (1953.17.134) is slightly paler, but warmer in colour above owing to the light brown edging to the feathers being wider than in the type ; the breast and flanks are correspondingly warmer and are washed a light brown. They are also slightly larger, particularly in the length of the wing and tail, but probably not enough to be recognized racially.

FIELD NOTE. During September they were seen in pairs on the lawn around the house at Nondugl and on the grasslands where they were very common. One bird was seen in partial display, it flew typically pipit-like into the sky and then volplaned down.

Saxicola caprata wahgiensis Mayr and Gilliard

Saxicola caprata wahgiensis Mayr and Gilliard, 1951, Amer. Mus. Novit. No. **1524**, p. 8. Mafulu, south-eastern New Guinea.

1953.17.139–142 ; 2 ♂, 2 ♀ ; Mount Giluwe, 7,300 ft.; May, June, 1951.

MEASUREMENTS : 2 ♂—wing, 77, 79 ; tail, 55, 56 ; bill, 11. 2 ♀—wing, 77, 78 ; tail, 56, 58 ; bill, 11. COLOURS : bill, black ; legs, black ; iris, brown-black. STOMACH CONTENTS : insects (grubs and adults).

" Two or three of these friendly stone-chats are usually to be seen around any building in the grasslands on the plateau. Their song is the first bird call to be heard in the early morning." (F. S.-M.).

Compared with the female specimen of *wahgiensis* collected by Mr. Gilliard at Nondugl the two females from Mount Giluwe are slightly darker below and on the sides of the neck. In the darker colour of the underparts these birds tend towards the Oranje Mountain bird, *belensis*, of which the females are larger than the present pair, Mayr and Gilliard (1951 : 8).

FIELD NOTE. Native name, " Kompichente ". A nest was found built on the ground on a pile of pit-pit roots and stems. It contained two juveniles with the feathers of the first plumage newly broken through the skin (26th September). Only the female was seen to visit the nest. A pair was seen in the garden perched on sticks in the flower beds, each dropped down to the ground from time to time to pick up insects. A fairly tame bird often seen in the Mount Hagen area.

Turdus poliocephalus erebus Mayr and Gilliard

Turdus poliocephalus erebus Mayr and Gilliard, 1952, Amer. Mus. Novit. No. **1577**, p. 7. New name for *Turdus poliocephalus carbonarius* Mayr and Gilliard, 1951, Amer. Mus. Novit. No. **1524**, p. 7. Mount Orata, Kubor Mountains, Central Highlands, New Guinea. (NOT *Turdus carbonarius* Lichtenstein, 1823.)

1953.17.143–146 ; 3 ♂, 1 ♀ ; Mount Giluwe, 11,000 ft.; April, 1951.

MEASUREMENTS : 3 ♂—wing, 124–132 ; tail, 90–94 ; bill, 20–21. 1 ♀—wing, 123 ; tail, 92 ; bill, 21. COLOURS : ♂—bill, orange-yellow with darker tips ; legs, orange ; iris, brown with yellow eye ring ; inside of mouth, orange. ♀—bill, upper mandible dark horn, lower mandible orange; legs, dull orange; iris, dark brown — yellow eye ring. STOMACH CONTENTS: berries and small beetles.

" On the top of Mount Giluwe the blackbird leaves the shelter of the small timber in the late afternoon and flies into the open alpine grassland where it searches among the rocks and tussock-grasses for its food." (F. S.-M.). The gonads of all the specimens were enlarged.

Melampitta lugubris longicauda Mayr and Gilliard

Melampitta lugubris longicauda Mayr and Gilliard, 1952, Amer. Mus. Novit. No. **1577**, p. 1. Mount Tafa, Wharton Range, south-eastern New Guinea.

1953.17.147–148; 1 juv. ♂, 1 ♀; Mount Giluwe, 9,000–8,500 ft.; April, 1951.

MEASUREMENTS: 1 juv. ♂—wing, 83; tail, 33; tarsus, 40; bill, 15. 1 ♀—wing, 84; tail, 54; tarsus, 39; bill 16. COLOURS: bill, black; legs, black; iris, dark brown. STOMACH CONTENTS: small insects.

The juvenile male is tawny black with the under-parts washed with honey-brown. Its primaries appear to be fully grown, but the central rectrices are absent.

Crateroscelis robusta robusta (De Vis).

Gerygone robusta De Vis, 1898, Ann. Rep. Brit. New Guinea, **1896–97**, p. 84. Wharton Range, south-eastern New Guinea.

1953.17.149–150; 2 ♂; Mount Giluwe, 8,000–7,500 ft.; June, 1951.

MEASUREMENTS: 2 ♂—wing, 64, 65; tail, 39, 40; bill, 12. COLOURS: bill, upper mandible dark horn and lower mandible light horn; legs, flesh; iris, yellow to orange-red.

Although these birds have been named *robusta* they differ from topotypical specimens by being more greyish in colour. In addition, the wing coverts, the lower part of the back, lower abdomen and flanks have a faint olivaceous wash. Mayr and Gilliard (1954 : 345) and Gyldenstolpe (1955 : 84) reported that among the birds from the Bismarck, Hagen and Kubor Mountains which they named *robusta* there was some variation in colour although a few specimens matched topotypical material. This pair from Mount Giluwe were sent to the Berlin Museum; there Professor Stresemann kindly compared them with the type of *albigula* Reichenow from Schraderberg in the Sepik Mountains, which is now regarded as a synonym of *robusta*. He found that they agreed with this specimen so it might appear that *albigula* is a valid race, but in view of the variation in the series collected by Mr. Gilliard and Count Gyldenstolpe I consider that it is better not to separate *albigula* on these two specimens.

Eupetes leucostictus loriae Salvadori

Eupetes loriae Salvadori, 1896, Ann. Mus. Civ. Genova, (2) **16**, (= **36**), p. 102. Moroka, south-eastern New Guinea.

1953.17.151, 153, 153*a*; 1 ♂, 1 ♀, 1 juv. ♀; Mount Giluwe, 8,500 ft.; May, June, 1951.

1953.17.152; 1 ♀; Hagen Range, 8,500 ft.; February, 1951.

MEASUREMENTS: 1 ♂—wing, 76; tail, 82; bill, 18. 2 ♀—wing, 84,86; tail, 94, 98; bill, 18, 19. 1 juv. ♀—wing, 82; tail, 84; bill, 17. COLOURS: bill, black; legs, brown-grey to brown-black; iris, dark brown.

These birds are completing moult or are in fresh plumage except the February bird, where the plumage is worn. They were taken in the forests of the north slopes of Mount Giluwe. Nearest to *loriae* but differ by being a clearer blue below, due to the green wash being restricted to the flanks, the sides of the thorax and to a small patch on the upper breast near the throat. (The blue, however, is not so bright as that of a specimen of *amabilis* received on loan from the American Museum of Natural History.) The upper-parts appear to be a brighter green, slightly less olivaceous in colour; this difference, however, may be due to fading on the part of the older specimens. The bills are somewhat more slender than in both topotypical *loriae* and *amabilis*, particularly the latter.

FIELD NOTE. Native name, "Penkeklempo" or "Kengnan" (the latter is probably the name for *E. castanonotus*). A nest was found in a hole about 2 ft. above the ground in a half-dead stump of a tree-fern. An adult continued to visit the nest frequently and did not appear to be shy although the porters were nearby. It searched for insects on the ground by turning over moss and leaves with a quick movement of the bill; insects that were taken were too small to be identified. It is possible that both parents feed the young because a second visit to the nest followed too soon upon the first for the same individual to have found food so quickly. When it returned to the nest the bird remained near the ground and jumped into the nest-hole from immediately beneath it. Faeces were removed from the nest on several occasions. The nest was situated so that no sunlight fell directly on it and the nest hole faced to the east. On 5th October some of the vegetation was removed to allow more light to fall on the nest and two young birds covered with a heavy grey down were discovered there. They crouched down in the middle of the nest at first, then they stretched out their necks and started to hiss in a snake-like manner. The nest was then observed from a short distance away, after a while the juveniles started to preen; but when the sun began to fall directly on to the nest the young birds began to shift around and utter a harsh cry. Finally they jumped out of the nest and one of the parents lead them away along a small run through the undergrowth. The nest itself was circular in shape, with an external diameter of about 145 mm. and an internal one of about 75 mm.. It was heavily built on an untidy foundation of sticks, ferns and dead leaves, the inner cup was composed of fine rootlets lined with the skeletons of leaves, although one green leaf was removed from the nest. A second nest was found containing two young birds on 8th October; these were about the same stage of development as the young in the first nest. It was situated in a nest-hole about 3 ft. from the ground and similarly built to the first one only with less foundation. Both of the parents fed the young. The gape of the juvenile was white and the inside of the mouth a pale orange. The young were fed eleven times in one hour at the height of feeding, but only five times between 11.50 and 12.50 hours. On one occasion one of the parents sat on the nest and started to brood the young, when the other came to feed the juveniles it pushed the brooding parent off the nest; there appeared to be no recognition behaviour. The adults were very tame and continued their search for insects to within an arm's length of the hide and ignored all noises that came from inside. A third nest was found in a hole towards the base of a tree-fern. In it were two eggs (16th October), Mayr and Gilliard (1954 : 345).

Ifrita kowaldi kowaldi (De Vis)

Todopsis kowaldi De Vis, 1890, Ann. Rep. Brit. New Guinea, **1888-89**, p. 59. Owen Stanley Mountains, south-eastern New Guinea.

FIELD NOTE. Native name, " Kompe-chicko ". A nest was found built about 12 ft. up in a slender sapling, it was thickly decorated with moss which gave it a massive appearance. In the nest there was one juvenile which seemed to suffer badly from the heat. Both parents fed the young bird ; once the juvenile was given a cicada-like insect which was so large that the parent seemed to have difficulty in forcing it down the young bird's throat.

Malurus alboscapulatus subspecies ?

Malurus alboscapulatus A. B. Meyer, 1874, Sitzungsber. Akad. Wiss. Wien, **69**, p. 469. Arfak Mountains, north-western New Guinea.

1953.17.154–157 ; 1 ♂, 2 juv. ♂, 1 ? ; Mount Giluwe, 7,500–7,300 ft.; April, June, 1951.

MEASUREMENTS : 3 ♂—wing, 51–53 ; tail, 50–59 ; bill, 11·5–12·5. 1 ?—wing, 49 ; tail, 57 ; bill, 11. COLOURS : bill, black (unsexed specimen, lower mandible dark horn) ; legs, dark horn ; iris, dark horn. STOMACH CONTENTS : insects.

Mayr and Gilliard (1954 : 346) and Gyldenstolpe (1955 : 88) reported that apart from wing size all the birds collected in the Wahgi region agreed with topotypical specimens of the race *mafulu* from the mountains of south-eastern New Guinea. It seems to me, however, that the adult male from Mount Giluwe is a closer match with a specimen of the longer winged race *balim* from the Snow Mountains which I had on loan from the American Musuem of Natural History than with a specimen of *mafulu*. But, again, the immature birds seem to be a fairly close match with young *mafulu*. The birds from Mount Giluwe are also larger than birds of the race *tappenbecki* (♂, wing, 45–48) from the lower Ramu and Sepik rivers north of the Schrader-Bismarck Range, an area considerably nearer than either the Snow Mountains or Mafulu. Professor Stresemann who kindly compared the series with topotypical specimens of *tappenbecki* in the Berlin Museum was able to separate the immature birds on colour as well as wing length.

Megalurus timoriensis subspecies ?

Megalurus timoriensis Wallace, 1863, Proc. Zool. Soc. Lond. **1863**, p. 489. Dilly, Timor.

SERIES A :

1953.17.158 ; 1 ♂ ; Mount Giluwe, 12,000 ft.; April, 1951.
1953.17.159–162 ; 1 juv. ♂, 3 ♀ ; Lamende Range, 11,000 ft.; May, 1951.

SERIES B:

1953.17.163–166; 4 ♂; Mount Giluwe, 7,300 ft.; April, 1951.

MEASUREMENTS: SERIES A: 2 ♂—wing, 73, 74; tail, 95·5, 96; bill, 12, 14. 3 ♀—wing, 68–71; tail, 93–97; bill, 12. SERIES B: 4 ♂—wing, 71–75; tail, 98–109; bill, 12–13. COLOURS: bill, upper mandible dark horn and the lower mandible pale horn; legs, brownish dark flesh; iris, SERIES A, light to dark brown—SERIES B, pale orange to light brown. STOMACH CONTENTS: insects.

Mayr and Gilliard (1951 : 9) described two races of this species of warbler from Mount Hagen. They named the birds of the summit (alpine) grasslands at 12,000 ft. *montanus* and those of the grass slopes at 7,800 ft. *wahgiensis*. The birds were separated mainly on the somewhat darker, more rufous, colouring of the light areas of the upper-parts of *montanus*. Through the kindness of the American Museum of Natural History I have examined two specimens of *montanus* and one of *wahgiensis* from the series on which the descriptions were based. The specimens in Series A and Series B listed above are distinguishable from each other and, as far as I can see, the high altitude series matches Mayr and Gilliards' lower altitude form *wahgiensis*, while the lower series on Mount Giluwe matches the high altitude *montanus*. The explanation of this curious reversal on two neighbouring peaks is not evident. It seems certain, at least, that the differences are not caused by seasonal changes in plumage for in both series there are birds in worn and fresh dress.

FIELD NOTE. Native name, " Kuchaill " (" ll " as in Welsh).

Cisticola exilis diminuta Mathews.

Cisticola exilis diminuta Mathews, 1922, Birds Austr. **9**, p. 373. Paterson Creek, Cape York, Queensland, Australia.

1953.17.167; 1 ♀; Mount Giluwe, 7,300 ft.; June, 1951.

MEASUREMENTS: 1 ♀—wing, 44; tail, 47; tarsus, 18; bill, 9·5. COLOURS: bill, horn colour, darker on ridge; legs, flesh colour; iris, dull brown. STOMACH CONTENTS: insects.

Generally regarded as being a species restricted to the grasslands below 4,000 ft. it is interesting that this specimen was taken at 7,300 ft.. The specimen is in winter plumage.

Sericornis perspicillatus Salvadori

Sericornis perspicillata Salvadori, 1896, Ann. Mus. Civ. Genova. (2) **16** (= **36**), p. 99. Moroka, south-eastern New Guinea.

FIELD NOTE. A somewhat pear-shaped nest was found in the forest near Tomba. It was about 2 to 3 ft. above the ground, hanging by a few fibres from a twig. The entrance to the nest was about half-way up one side; above it a small bulge formed a " porch ". Two young birds were in the nest (15th October). Both parents fed the young and during a period of one hour 16 visits were made with food ; nest sanitation occurring 3 times. During another period of watching for 30 minutes food was taken to the nest 7 times. Among the insects fed to the juveniles a moth, a small green caterpillar and a Tipulid were identified. The adults chattered noisily around the nest. They were active and seldom remained still, hopping around in the undergrowth and sideways up the stems of the bushes. They flirted their wings constantly, like birds of the genus *Phylloscopus*.

Gerygone ruficollis insperata De Vis

Gerygone insperata De Vis, 1892, Ann. Rep. Brit. New Guinea, **1890-91**, p. 94. Mount Suckling, south-eastern New Guinea.

FIELD NOTE. Native name, " W'un-monamp ". A domed nest containing two fully-fledged juveniles was found on 3rd October in the forest near an area of swampland. One point of interest is that three different adults appeared to feed the young birds. Apart from this the behaviour of the adults was typical of most warblers ; they flitted with quick movements from branch to branch and never remained still for any length of time. Both the young and the adults were very noisy.

Peltops montanus Stresemann

Peltops blainvillii montanus Stresemann, 1921, Anz. Ornith. Ges. Bayern, **1**, p. 35. Hunsteinspitze, Sepik Mountains, northern New Guinea.

FIELD NOTE. One bird was seen in the forest at the top of a high tree, the identity of this blackbird with a white patch below and behind each eye and the crimson rump and vent was unmistakable.

Rhipidura brachyrhyncha devisi North

Rhipidura devisi North, 1897, Proc. Linn. Soc. New South Wales, **22**, p. 444. New name for *Rhipidura albicauda* De Vis, 1897, Ibis, p. 375. No type locality given (= ? Mt. Scratchley). (NOT *Rhipidura albicauda* North, 1895).

1953.17.168 ; 1 imm. ♂ ; Mount Giluwe, 7,500 ft.; June, 1951.

MEASUREMENTS : 1 imm. ♂—wing, 71·5 ; tail, 92 ; tarsus, 24 ; bill, 8. COLOURS : bill, upper mandible dark horn, lower mandible light horn ; legs, pale flesh ; iris, brown-black. STOMACH CONTENTS : insects.

Rhipidura albolimbata lorentzi van Oort

Rhipidura albo-limbata lorentzi van Oort, 1909, Nova Guinea, **9**, (Zool.), p. 85. Hellwig Mountains, Oranje Range, New Guinea.

1953.17.169 ; 1 ♀ ; Mount Giluwe, 8,000 ft.; June, 1951.

MEASUREMENTS : 1 ♀—wing, 82 ; tail, 85 ; bill, 10. COLOURS : bill, *not recorded ;* legs, black ; iris, brown-black. STOMACH CONTENTS : insects.

FIELD NOTE. Native name, "Ipenem". Two nests were found, one was built about 20 ft. above the ground in a tree, the other about 12 ft. up in a creeper. Each was a small neat cup with a "tail", the outsides were close-knit in appearance as if spiders' webs had been woven in. Both nests contained young (26th September) which the adults continued to feed while the party stood beneath the nests.

Rhipidura leucophrys melaleuca (Quoy and Gaimard)

Muscipeta melaleuca Quoy and Gaimard, 1830, Voy. Astrolabe, Zool. **1**, p. 180. New Ireland.

1953.17.170; 1 ♂; Mount Giluwe, 7,300 ft.; June, 1951.

MEASUREMENTS: 1 ♂—wing, 104; tail, 103; tarsus, 25; bill, 13. COLOURS: bill, black; legs, black; iris, brown-black. STOMACH CONTENTS: insects.

Usually regarded as a bird of the coast, lowland lakes, swamps and rivers it is interesting that Mr. Shaw-Mayer found it to be "fairly plentiful" on the high plateau near Mount Giluwe. Mayr and Gilliard (1954: 348) reported that it was common at Nondugl at 5,000 ft., and that it was nesting at 7,000 ft.

FIELD NOTE. A common bird which spends most of the time on the ground. The tail is not spread out much compared with many other members of the genus. When the bird jumps up to a perch from the ground the long tail is swung pendulum-fashion in the manner of that of a shrike.

Machaerirhynchus nigripectus saturatus Rothschild and Hartert

Machaerirhynchus nigripectus saturatus Rothschild and Hartert, 1913, Novit. Zool. **20**, p. 498. Mount Goliath, Snow Mountains, New Guinea.

1953.17.171; 1 ♂; Mount Giluwe, 8,000 ft.; May, 1951.

MEASUREMENTS: 1 ♂—wing, 64; tail, 62; bill, 11. COLOURS: bill, black; legs, black; iris, black-brown. STOMACH CONTENTS: small insects.

FIELD NOTE. Native name, "Koongnarémp". Fairly common in the forest.

Microeca papanua Meyer

Microeca papuana A. B. Meyer, 1875, (April), Sitzungsber. Abh. Nat. Ges. Isis, Dresden, **1875**, p. 74. Arfak Mountains, north-western New Guinea.

1953.17.172; 1 ♂; Mount Giluwe, 7,500 ft.; May, 1951.

MEASUREMENTS: 1 ♂—wing, 78·5; tail, 48; bill, 10. COLOURS: bill, black; legs, yellow; iris, dark brown. STOMACH CONTENTS: insects.

This specimen is a little larger and darker in colour than the other birds of this species that I have seen and there is marked reduction in yellow on the outer webs of the primaries. Rand (1942*b*: 483) reported similar differences in the birds he collected in the mountains of Dutch New Guinea and correlated the increase in size with altitude. He suggested that his birds appeared to be darker because the material with which they were being compared was foxed, and this may well account for the colour difference between the birds before me.

Petroica bivittata bivittata De Vis.

Petroeca bivittata De Vis, 1897, Ibis, p. 376. Mount Scratchley, south-eastern New Guinea.

1953.17.173, 176 ; 1 ♂, 1 ? ; Mount Giluwe, 11,000–10,000 ft.; April, May, 1951.
1953.17.174–175 ; 2 ♂ ; Lamende Range, 11,000 ft.; May, 1951.

MEASUREMENTS : 3 ♂—wing, 73–77 ; tail, 46–48 ; bill, 9·0. 1 ?—wing, 73 ; tail, 45 ; bill, 9·0. COLOURS : bill, black ; legs, black ; iris, dark brown. STOMACH CONTENTS : small insects.

The April bird (sex ?) has started moulting, one bird taken in May is in fresh plumage the other two are completing moult. Collected on the alpine grasslands.

Peneothello sigillatus subspecies ?

Poecilodryas (?) *sigillatus* De Vis, 1890, Ann. Rep. Brit. New Guinea, **1888–89**, p. 59. Mount Victoria, south-eastern New Guinea.

FIELD NOTE. An adult female was seen on 18th October on an empty nest which was half concealed in moss and creeper. The nest was built of moss, green ferns and rootlets, with a thick lining of moss and dead fern leaves. It measured approximately 50 mm. in diameter internally and 115 mm. externally, the cup being about 25 mm. deep.

Peneothello cyanus subcyaneus (De Vis)

Poecilodryas subcyanea De Vis, 1897, Ibis, Ser. 7, **3**, p. 377. Mountains of south-eastern New Guinea.

1953.17.177 ; 1 ♂ ; Mount Giluwe, 7,500 ft.; May, 1951.

MEASUREMENTS : 1 ♂—wing, 99 ; tail, 68 ; bill, 15. COLOURS : bill, black ; legs, black ; iris, brown-black. STOMACH CONTENTS : small insects.

FIELD NOTE. Native name, " Goorgla ". Nests were built in the forks of upright branches in the bushes, and appeared to be made mainly of fine rootlets covered with moss and lined with dried fern fronds. They were round and deep, being about 55 mm. in diameter and 45 mm. deep internally and 130 mm. in diameter and 80 mm. high externally. One nest, first examined on 18th September, contained one juvenile almost ready to fly ; it was visited daily until 22nd September, when the young bird had flown. Another nest had one juvenile in it on 28th September, but this bird had flown when the nest was examined on the following day. An egg was found in a nest 17th October. It was a pointed oval with a light olive ground colour ; there were a few scattered dark brown spots and a fainter red-brown speckling that became more intense towards the broader end.

Heteromyias albispecularis centralis Rand.

Heteromyias albispecularis centralis Rand, 1940, Amer. Mus. Novit. No. **1074**, p. 4. Near Bernhard Camp, Idenburg River, at 2,150 m., central New Guinea.

1953.17.178–180 ; 1 ♂, 1 juv. ♂, 1 ♀ ; Mount Giluwe, 8,000–7,800 ft.; April, June, 1951.

MEASUREMENTS : 2 ♂—wing, 99, 101 ; tail, 61, 62 ; bill, 17, 18. 1 ♀—wing, 98 ; tail, 58 ; bill, 17. COLOURS : bill, black with tip pale horn (juv. ♂, pale horn) ; legs, flesh ; iris, dark brown. STOMACH CONTENTS : small beetles and other insects.

The two April birds are completing moult, although a few juvenile feathers still remain in the young male. The adult male (June) is in fresh plumage.

FIELD NOTE. Native name " Yamari." Several nests were found in dark parts of the moss forest where the light-meter read as low as 3·2 foot-candles for the most of one forenoon. They were built 7 to 10 ft. above the ground in the upper branches of young saplings, although one was found in a small bush where it was only 3 ft. from the ground. The nests appeared to be very similar in being heavily built on slender branches, which in some cases could not adequately support their weight. One nest that was examined was found to be about 90 mm. in diameter and 40 mm. deep ; it was built of grass and twigs with a little moss and lined with thin fern rootlets. All the nests contained young birds. One juvenile examined on 20th September was blackish brown above with the shafts of the feathers lighter in colour. The breast was brown and the belly white with a brown wash. The gape and the inside of the mouth were yellow. The legs, which were long and strong, were flesh coloured. The irides were brown. Another nest, seen two days later on 22nd September, contained only one nestling which was quite naked ; yet a week later, on 29th September, a nest was found with one juvenile which had well-grown wing quills. This young bird rose on its legs and with arched wings started to cheep when the parents returned to the nest. It was established that both parents fed the young whose main diet appeared to consist of earthworms. On two occasions a juvenile was seen to eject a bag of faeces on to the rim of the nest, one of the adults returned to the nest expressly to remove it—or so it appeared. The adults were never seen in the forest except at the nest. Sometimes they would return to the nest silently, at other times they would call quietly with a soft, musical piping sound. The young always answered this call, but not loudly. When the adult made this piping call the throat vibrated, but the bill remained closed. The alarm call was, " kak-kaktak-kak ". Once when a nest was being examined an adult repeatedly exhibited a distraction display by " injury feigning " on the ground where it dragged one wing as if it were broken.

The adults had a habit of remaining hidden in the undergrowth and of standing quietly on the nests, a form of behaviour that is more characteristic of a babbler than a flycatcher. The bird's long strong legs and heavy bill are other characters that suggest that this bird may have some affinity with the Timalinae. As opposed to these Timaloid tendencies adults were seen to perch sideways on the moss-covered trunks of the trees in a position curiously like that of a nuthatch.

Pachycephala schlegelii obscurior Hartert

Pachycephala schlegelii obscurior Hartert, 1896, Novit. Zool. **3**, p. 15. Eafa District, Owen Stanley Mountains, south-eastern New Guinea.

1953.17.181 ; 1 ♂ ; Mount Giluwe, 7,500 ft.; May, 1951.

MEASUREMENTS : 1 ♂—wing, 88 ; tail, 65 ; bill, 11. COLOURS : bill, black ; legs, brown-black ; iris, brown-black. STOMACH CONTENTS : insects.

Pachycephala modesta hypoleuca Reichenow

Pachycephala hypoleuca Reichenow, 1915, Journ. f. Ornith. **63**, p. 125. Schraderberg, Sepik Mountains, northern New Guinea.

1953.17.182–183 ; 1 ♂, 1 ♀ ; Lamende Range, 11,000 ft.; May, 1951.

MEASUREMENTS : 1 ♂—wing, 90 ; tail, 64 ; bill, 11. 1 ♀—wing, 89 ; tail, 65 ; bill, 12. COLOURS : bill, black ; legs, dark grey to black ; iris, dark brown. STOMACH CONTENTS : small grubs and insects.

These specimens were collected among the small trees on the alpine grasslands.

Pachycephala rufinucha niveifrons Hartert

Pachycephala rufinucha niveifrons Hartert, 1930, Novit. Zool. **36**, p. 57. Wondiwoi, Wandammen Mountains, north-western New Guinea.

1953.17.184 ; 1 juv. ♂ ; Hagen Range, 8,000 ft.; March, 1951.

1953.17.185–186 ; 2 ♂ ; Mount Giluwe, 8,000–7,8000 ft.; April, 1951.

MEASUREMENTS : 3 ♂—wing, 89–91 ; tail, 68–70 ; bill, 16·5, (juv., 14). COLOURS : bill, black (juv., horn) ; legs, olivaceous grey-black (juv., horn) ; iris, yellow (juv., dark grey). STOMACH CONTENTS : insects.

Apart from having slightly longer wings these birds match material taken at lower altitudes on the Utakwa River (wing, 84–86). Rand (1942*b* : 489) showed that in this species wing length could be correlated with altitude, the birds from the higher altitudes being slightly larger.

FIELD NOTE. A nest was built in a fork of a branch about 7 ft. up in a bush. The outer part of the nest was made of ferns, coarse rootlets and green moss, the inner part of the thin fibres, fine rootlets and the skeletons of leaves. There were two well incubated eggs in the nest on 17th October. These were a chalky white colour with black spots and a fainter underlay of grey spots. Another nest found two days later, on 19th October, contained two juveniles ; the insides of their mouths were a pale orange apart from two prominent blue spots at the posterior of the palate. It is probable that the young were fed by both parents, but the nest was visited only infrequently. During a three and a half hour watch on the nest an adult visited it only four times during the first half hour, three times during the second, once during the third but four times during the last half-an-hour.

Myiolestes megarhynchus tappenbecki (Reichenow)

Colluricincla tappenbecki Reichenow, 1899, Journ. f. Ornith. **47**, p. 118. Friedrich Wilhelms Hafen (= Madang), Astrolabe Bay, north-eastern New Guinea.

1953.17.187–190 ; 2 ♂, 2 ♀ ; Minj, Wahgi River, 5,000 ft.; November, 1950.
1953.17.191 ; 1 ♀ ; Mount Giluwe, 7,5000 ft.; May, 1951.

MEASUREMENTS : 2 ♂—wing, 94, 96 ; tail, 76, 79 ; bill, 20, 21. 3 ♀—wing, 91—92 ; tail, 72—76 ; bill, 18—19. COLOURS : bill, 2 ♂, brown horn—3 ♀, horn ; legs, blue-grey to dark grey ; iris, brown. STOMACH CONTENTS : insects ; 1 ♂, small (?)water snail.

All the four birds taken at Minj in November, 1950, were taken on the nest, the nests being built about one foot above the ground in long grass. It is interesting to note that these four birds are in different plumages. The two males are in full moult ; and of the two November females one is in worn dress while the other is in fresh plumage. The plumage of the female taken in May shows some signs of wear.

Eulacestoma nigropectus subspecies ?

Eulacestoma nigropectus De Vis, 1894, Ann. Rep. Brit. New Guinea, **1893–94**, p. 102. Mount Maneao, south-eastern New Guinea.

1953.17.192 ; ♀ ? ; Mount Giluwe, 8,000 ft.; May, 1951.

MEASUREMENTS : 1 ♀ ?—wing, 71 ; tail, 52 ; bill, 11·5. COLOURS : bill, horn ; legs, purple-flesh ; iris, grey-brown. STOMACH CONTENTS : insects.

This is a juvenile, and in the absence of comparable material I cannot name it racially. It is probably *clara* Stresemann and Paludan as Mayr and Gilliard (1954 : 354) reported that their birds from this area were that race.

Lanius schach stresemanni Mertens

Lanius schach stresemanni Mertens, 1923, Senckenbergiana, **5**, p. 228. Kulungtufu, Saruwaged Mountains, north-eastern New Guinea.

1953.17.193, 195–196 ; 1 ♂, 2 ♀ ; Mount Giluwe, 7,300 ft.; May, June, 1951.
1953.17.194 ; 1 juv. ♂ ; Wahgi River, 5,200 ft.; November, 1950.

MEASUREMENTS : 1 ♂—wing, 101 ; tail, 140 ; bill, 16. 1 juv. ♂—wing, 95 ; tail, 105 ; bill, 13. 2 ♀—wing, 97, 98 ; tail, 121, 123 ; bill, 15. COLOURS : bill, black (juv. ♂, lower mandible, horn) ; legs, black ; iris, brown-black. STOMACH CONTENTS : small grubs, beetles and other insects.

" Not many of this solitary species on the grasslands of the plateau. A bird here and there, as usual clinging to the stem of cane-grass." (F. S.-M.). The adult male is in fresh plumage and the testes are slightly enlarged. The plumage of the young male is worn. The two females are completing moult with the outer primaries growing.

FIELD NOTE. Native name, " Komkompir ". Two deep-cupped nests, built about 6 ft. above the ground, were found in tall reeds. One, examined on 5th September, contained two eggs; but in the other, found on 23rd September in pit-pit country, were two well-grown juveniles.

Artamus maximus Meyer

Artamus maximus A. B. Meyer, 1874, Sitzungsber. Akad. Wiss. Wien, **69**, p. 203. Hatam, Arfak Mountains, north-western New Guinea.

1953.17.197 ; 1 ♂ ; Minj, Wahgi River, 5,000 ft.; November, 1950.

MEASUREMENTS : 1 ♂—wing, 164 ; tail, 73 ; bill, 23. COLOURS : bill, blue-grey ; legs, grey ; iris, dark brown. STOMACH CONTENTS : small beetles.

Gyldenstolpe (1955 : 121) separated *A. m. wahgiensis* mainly on the darker colour of the upper-parts of the birds from the Wahgi region in comparison with a series from the Arfak Mountains. The present specimen, however, hardly differs from the Arfak Mountain bird. The only variations in colour in the specimens I have examined appear to be correlated with age and season. In a series from south-eastern New Guinea there are some individuals lighter in colour than both the Wahgi River and Arfak birds, and others that are darker in colour. It seems that the lighter coloured birds are juveniles or adults in worn, faded plumage ; while the darker birds are adults in fresh plumage. Unfortunately this series is incomplete in specimens taken in all months of the year, so the degree of seasonal variation cannot be established with certainty. As the individual variation is greater than that between the birds from the Central Highlands and the Arfak Mountains, I am not naming the present bird racially.

FIELD NOTE. Native name, " Kompurkaikir ". A nest was built about 50 ft. above the ground in the fork at the base of an upright branch of a dead tree in the forest. Three juveniles, almost ready to fly, were found in it (26th September). It is interesting that four or five different adults were observed to feed the young, and on one occasion three adults were seen on the nest at the same time ! Communal nesting of this nature is rare and provides a subject for further investigation. Like many other communities this one was very noisy, with both the adults and the juveniles contributing to the chatter. The juvenile plumage was similar to that of the adult, but the dark areas of the body were flecked with a light brown ; the bill of the young bird was horn coloured.

Aplonis metallica metallica (Temminck)

Lamprotornis metallicus Temminck, 1824, Planch. Col. d'Ois, pl. 266. " Celebes," by error for Amboina, Moluccas.

1953.17.198 ; 1 ♀ ; Mount Giluwe, 7,000 ft.; May, 1951.

MEASUREMENTS : 1 ♀—wing, 104 ; tail, 91 ; bill, 16. COLOURS : bill, black ; legs, black ; iris, bright orange-red.

" Few *Aplonis* were seen at 7,000 feet when this specimen was taken in the woodlands but the bird was plentiful at 5,300 feet." (F. S.-M.).

Pomareopsis briujni (Salvadori)

Grallina bruijni Salvadori, 1875, Ann. Mus. Civ. Genova, **7**, p. 929. Arfak Mountains, northwestern New Guinea.

FIELD NOTE. Native name, " Notechll " (" ll " as in Welsh). This is a bird of the mountain stream, and one was seen by a rushing torrent at about 6,500 ft. When it alighted on a rock it fanned out its tail in the same manner as the Plumbeous Redstart, *Pheonicurus fuliginosus*, of the fast-flowing streams of the Himalayas.

Epimachus meyeri bloodi Mayr and Gilliard

Epimachus meyeri bloodi Mayr and Gilliard, 1951, Amer. Mus. Novit. No. **1524**, p. 10. Mount Hagen, Central Highlands, 8,300 ft., New Guinea.

1953.17.199–200 ; 1 ♂, 1 juv. ♂ ; Hagen Range, 9,000 ft.; February, 1951.

1953.17.201 ; 1 ♀ ; Mount Wilhelm, Bismarck Range, 8,000 ft.; May, 1951.

MEASUREMENTS : 1 ♂—wing, 174 ; tail, 604 ; bill, 78. 1 juv.♂—wing, 149 ; tail, 320 ; bill, 60. 1 ♀—wing, 149 ; tail, 312 ; bill, 76. COLOURS : bill, black ; legs, dark grey (ad. ♂ black) ; iris, blue-grey. STOMACH CONTENTS : fruits.

The juvenile male resembles a series of adult females from the Hagen Range except in the length of the bill. The adult female from the Bismarck Range differs from this series in the upper-parts being lighter, less olivaceous, more like the ochraceous colour of the females of *meyeri*. Not until more material is available from the Bismarck Range will it be possible to assess the importance of this difference, but it may be that the Wahgi Gap country plays just as an important part in the distribution of the races of *E. meyeri* as it does in the distribution of the races of *Astrapia stephaniae*, (see below). The plumage of the present birds is fairly fresh, showing little signs of wear. Specimens taken in October in previous collections from Mount Hagen are in worn plumage and those taken in November are in full moult. It appears from the stomach contents of the birds that *E. meyeri* is not entirely frugivorous, for the stomachs of adult birds have been found to contain berries, grasshoppers and other insects in addition to various fruits.

Astrapia stephaniae femina Neumann

Astrapia stephaniae femina Neumann, 1922, Verh. Ornith. Ges. Bayern, **15**, p. 236. Schraderberg, Sepik Mountains, 60 miles north of the Hagen Mountains, northern New Guinea.

1953.17.202; 1 ♀; Mount Wilhelm, 8,000 ft.; May, 1950.

MEASUREMENTS: 1 ♀—wing, 145; tail, 320; bill, 24. COLOURS: bill, black; legs, blue-grey (feet, black); iris, black-brown. STOMACH CONTENTS: fruits.

Mayr and Gilliard (1952*a*) showed that the grasslands between the Hagen Range and the mountains of the Wahgi Divide (a westerly spur of the Bismarck Range) acted as a barrier in the distribution of *A. mayeri*, a species closely related to *A. stephaniae*. The same authors (1954 : 321) also described the deforestation in the Wahgi Valley, which they suggested formed another important barrier to forest birds. It appears, then, that the mountain forest birds of the Kubor Range along the south and the Hagen Range at the head of the Wahgi Valley are isolated by open country from the mountain forest birds of the Wahgi Divide and the Bismarck Range north of the valley. This barrier apparently influences the distribution of the races of *A. stephaniae*, for specimens collected in the Bismarck Range by Mr. F. Shaw-Mayer in 1946 have been matched with cotypical material of *femina*, and Gyldenstolpe (1955 : 127) identified his birds from north of the Wahgi Valley as this race. On the other hand, two specimens from Mount Giluwe (see below) appear to be *ducalis*, which is the race found to the south of the valley in the Kubor Range (Mayr and Gilliard, 1954 : 356). The adult females from the Bismarck Range are slightly more olivaceous above than the adult females of *ducalis* and the under-parts are rust coloured barred with black instead of a buffy colour barred with black. In the colour of the under-parts they agree with the differential characters given by Mayr and Gilliard (1954 : 356). (They do not, however, exhibit the subobsolete white streaks at the bases of the central tail feathers described by these authors.) The present specimen differs somewhat from other material in having a narrow chestnut collar barred with black across the shoulders, the colour of the collar becoming lighter laterally as it merges into the rust barred-black of the breast.

Astrapia stephaniae ducalis Mayr

Astrapia stephaniae ducalis Mayr, 1931, Mitt. Zool. Mus. Berlin, **17**, p. 711. Dawong, Herzog Mountains, eastern New Guinea.

1953.17.203–204; 1 ♂, 1 ♀; Mount Giluwe, 8,500 ft.; March, April, 1951.

MEASUREMENTS: 1 ♂—wing, 165; tail, 660; bill, 20. 1 ♀—wing, 137; tail, 320; bill, 21. COLOURS: bill, black; legs, dark grey; iris, brown-black. STOMACH CONTENTS: fruits and berries.

FIELD NOTE. Five birds, females or immature males, were seen in the forest. In flight, with their long tails streaming behind, they were reminiscent of the Racquet-tailed Drongo, *Dissemurus paradiseus*; the diving flight being particularly like that of the Dicruridae. The birds appeared to be hunting for insects in the moss covering the branches of the trees ; one bird was seen to swallow what was probably a spider.

Astrapia mayeri Stonor

Astrapia mayeri Stonor, 1939, Bull. Brit. Ornith. Club, **59**, p. 57. " Eighty to a hundred miles west of Mount Hagen," central New Guinea.

1953.17.205 ; 1 ♂ ; Mount Giluwe, 9,000 ft.; March, 1951.

1953.17.206–207 ; 1 juv. ♂, 1 ♀ ; Hagen Range, 9,000–8,500 ft.; December, 1950.

MEASUREMENTS : 1 ♂—wing, 177 ; tail, 852 ; bill, 13. 1 juv. ♂—wing, 170 ; tail, 350 ; bill, 12. 1 ♀—wing, 148 ; tail, 310 ; bill, 15. COLOURS : bill, black ; legs, blue-grey (feet, black) ; iris, brown-black. STOMACH CONTENTS : fruits and green berries.

FIELD NOTE. The branches of the forest trees on which the bird perches are thickly covered with moss. It is probably this layer of moss that prevents the long tail feathers from becoming damaged.

Astrapia stephaniae* × *Astrapia mayeri

1953.17.208 ; 1 ♂ ; Hagen Range, 8,000 ft.; March, 1951.

MEASUREMENTS : 1 ♂—wing, 167 ; tail, 821 ; bill, 18. COLOURS : bill, black ; legs, dark grey (feet black) ; iris, brown-black.

Close to *mayeri* in having the tail white for most of its length ; but the rachis of the distal two-thirds of the central rectrices are brown in colour, and the webs of these feathers are fringed irregularly with brown. The nasal tuft is reduced in size to that of an immature male of *mayeri*, that is intermediate between the condition in *meyeri* where the tuft is present and in *stephaniae* where it is absent. The primaries are darker than in *mayeri*, being a solid black with a purple lustre like those of *stephaniae*. Too much importance should not be attached to the proportion of hybrid specimens in collections, for in the field they occur in a limited area which happens to be one of the most accessible. Mr. Shaw-Mayer wrote (in correspondence 5th November, 1952) of the difficulties he had experienced in obtaining a series of hybrids, and that, " Over the greater part of their extensive range the species *remain distinct*. The overlapping areas where hybridism takes place are small. . . . ".

Paradisaea apoda salvadorii Mayr and Rand

Paradisaea apoda salvadorii Mayr and Rand, 1935, Amer. Mus. Novit. No. **814**, p. 11. Vanumai, Central Division Papua, south-eastern New Guinea.

1953.17.209. 1 ♀ Wahgi River, 5,500 ft.; November, 1950.

MEASUREMENTS : 1 ♀—wing, 161 ; tail, 118 ; bill, 32. COLOURS : bill, blue-grey ; legs, brown-horn ; iris, bright yellow. STOMACH CONTENTS : fruits.

" Count Raggi's Bird-of-Paradise was fairly plentiful on the Wahgi River plateau ; finding sanctuary in the casuarina groves, small stands of secondary forest and in the few remnants left of the original oak forests. By mid-November (1950) they were breeding and several nests were observed ; in nearly every case the nests were high up, 50 to 60 feet, in casuarina trees. Each nest contained only one egg." (F. S.-M.).

Pteridophora alberti hallstromi Mayr and Gilliard

Pteridophora alberti hallstromi Mayr and Gilliard, 1951, Amer. Mus. Novit. No. **1524**, p. 12. Near Tomba, Hagen Range, Central Highlands, New Guinea.

1953.17.210 ; 1 juv. ♂ ; Mount Wilhelm, 7,500 ft.; May, 1950.
1953.17.211 ; 1 ♀ ; Hagen Range, 9,000 ft.; February, 1951.

MEASUREMENTS : 1 juv. ♂—wing, 112 ; tail, 80 ; bill, 15. 1 ♀—wing, 122 ; tail, 81 ; bill, 15. COLOURS : bill, black ; legs, brown-black (juv. ♂, grey-brown) iris, dark brown ; inside of mouth of ♀, green. STOMACH CONTENTS : green berries.

FIELD NOTE. Native name, " Kongbuk " (adult male) ; " Doongbi " (adult female and juveniles). An adult male was seen in the forest at about 7,000 ft. The bird was preening and called occasionally, the sound was like the squeaking of rusty iron. The long head plumes were manoevured to avoid the branches of the tree. A solitary bird.

Loria loriae amethystina Stresemann

Loria loriae amethystina Stresemann, 1934, Ornith. Monatsber. **42**, p. 144. Schraderburg, Sepik Mountains, northern New Guinea.

1953.17.212 ; 1 ♂ ; Mount Wilhelm, 6,500 ft.; May, 1950.
1953.17.213 ; 1 ♂ ; Hagen Range, 9,000 ft.; February, 1951.

MEASUREMENTS : 2 ♂ –wing, 103, 106 ; tail, 71, 72 ; bill, 15·5, 16. COLOURS : bill, black ; mouth-wattles, creamy white ; legs, dark olive ; iris, dark brown. STOMACH CONTENTS : berries.

FIELD NOTE. A domed nest with an exceptionally wide round opening was built about 12 ft. up in a decayed tree-stump in the forest. It was deep-set in living moss and built of green ferns and moss with a lining of fern stalks. There was one juvenile in the nest (25th September). Its head and breast were a smoke-grey and the wings a darker grey ; the gape and the inside of the mouth were white in colour. While the nest was being watched during the early part of one morning the female returned about every 10 to 15 minutes to feed the young and called with a soft " wark, wark " each time she approached. The food was regurgitated and appeared to consist of large berries and plum-coloured fruits. A short while after being fed the young bird expelled the fruit stones from its crop, they were ejected with a force sufficient to shoot them out through the mouth of the nest. Faecal capsules were also ejected occasionally from the nest, but generally the female assisted with nest sanitation. When the nest was examined a few days later it was deserted and contained faeces and fruit stones.

Cnemophilus macgregorii kuboriensis Mayr and Gilliard

Cnemophilus macgregorii kuboriensis Mayr and Gilliard, 1954, Bull. Amer. Mus. Nat. Hist. **103**, p. 361. Mount Orata, Kubor Mountains, Central Highlands, New Guinea, + 9,000 ft.

1953.17.214 ; 1 ♂ ; Minj River, Kubor Range ; 8,000–9,000 ft.; October, 1950.
MEASUREMENTS : 1 ♂—wing, 109 ; tail, 88 ; bill, 13 ; crest, 37. COLOURS : bill, black ; legs, dark olive ; iris, dark brown. STOMACH CONTENTS : fruits.

Mayr and Gilliard separated this race on the paler colour of the upper-parts in comparison with *sanguineus* from Mount Hagen. In colour it is closer to the scarlet-vermilion of *sanguineus* than the pale orange of *macgregorii* from south-eastern New Guinea ; the colour of *kuboriensis* being orange-vermilion. This specimen was taken near the headwaters of the Minj River and it matches a series from the Bismarck Range, which suggests that there may be an east to west cline from the pale colour of *macgregorii* in the south-east to the deep, rich colour of *sanguineus* from the Hagen Range. The series consists of birds in new and worn plumage but there is little seasonal colour difference.

Cnemophilus macgregorii sanguineus Iredale

Cnemophilus macgregorii sanguineus Iredale, 1948, Australian Zool. **11**, p. 162. Kumdi, Mount Hagen district, Central Highlands, New Guinea.

1953.17.215 ; 1 juv. ♂ ; Hagen Range, 9,000 ft.; February, 1951.
1953.17.216 ; 1 imm. ♂ ; Mount Giluwe, 9,000 ft.; May, 1951.
MEASUREMENTS : 1 imm. ♂—wing, 109 ; tail, 85 ; bill, 20 ; crest, 36. 1 juv. ♂—wing, 113 ; tail, 87 ; bill, 20 ; crest, 21. COLOURS : bill, black (juv. ♂, tip dark horn) ; legs, brown-black to glossy black ; iris, dark brown (juv. ♂, dull grey). STOMACH CONTENTS : fruits.

The young bird is a juvenile and indistinguishable from an adult female. The immature bird could well be described as " sub-adult ", for in colour it is intermediate between the young bird and an adult male, but the collector has indicated on the field label that the testes were as large as those of a breeding adult male. From this it seems that the bird comes into breeding condition before it is fully adult. If this is so it would be interesting to determine its behaviour towards an adult female and her response. The primaries and rectrices of this specimen are as richly coloured as topotypical *sanguineus ;* that is, darker than *kuboriensis* where these feathers are nearer the colour of *macgregorii.* It is on this character that I have been able to determine the racial identity of the bird.

Archboldia papuensis sanfordi Mayr and Gilliard

Archboldia papuensis sanfordi Mayr and Gilliard, 1950, Amer. Mus. Novit., No. **1473**, p. 1. Four miles west of Tomba, south-western slope of Mount Hagen, Central Highlands, New Guinea.

1953.17.217, 218, 220, 222 ; 3 ♂, 1 imm. ♂ ; Mount Giluwe, 9,000–8,500 ft.; March, April, May, 1951.

1953.17.219, 221, 223, ; 1 ♂, 1 juv. ♂, 1 imm. ♀ ; Hagen Range, 9,000–8,800 feet ; April, 1951.

MEASUREMENTS : 4 ♂—wing, 165–171 ; tail, 167–171 ; bill, 17–20. 1 juv. ♂—wing, 142 ; tail, 131 ; bill, 19. 1 imm. ♂—wing, 163 ; tail, 141 ; bill, 22. 1 imm. ♀—wing, 154 ; tail, 132 ; bill, 19. COLOURS : bill, black ; legs, grey-blue (imm. ♀, bright light blue) ; iris, dark brown. STOMACH CONTENTS : fruits.

These are the first specimens of this genus to be received by the British Museum (Natural History). In comparison with the description of this race the feathers of the crest in the male exhibit some variation. Although they are predominantly black-based with orange-gold tips some have an area of white between the black and the orange-gold and a few are tipped with black. All the specimens are in moult.

FIELD NOTE.—Near Tomba an area of the forest floor had been cleared to form a bower measuring approximately 5 ft. by 4 ft. The branches of the surrounding trees and a fallen tree trunk were densely decorated with the bamboo-like trailing vines of epiphytes which grow on high trees. Several branches were quite bare and smooth, probably from wear when the birds alighted and postured. The floor of the bower was strewn with the dead fronds of ferns. A number of shells of land snails were also found on the ground.

Amblyornis macgregoriae De Vis

(Text-fig 2)

Amblyornis macgregoriae De Vis, 1890 (22nd February), Ann. Rep. Brit. New Guinea, **1888–89**, p. 61. Musgrave Range, south-eastern New Guinea.

1953.17.224 ; 1 ♂ ; Kubor Range, 7,000 ft.; November, 1950.
1953.17.225–226 ; 1♂, 1 juv.♂; Hagen Range, 9,000 ft.; February, 1951.
1953.17.227 1 ♂ ; Lamende Range, 9,000 ft.; June, 1951.

MEASUREMENTS : 4 ♂—wing, 134–137 ; tail, 83–86 ; bill, 17–19 ; crest, 60–65. COLOURS : bill, dark horn lighter towards base ; legs, dark olive-brown ; iris, dark brown. STOMACH CONTENTS : fruits.

Mayr and Gilliard (1954 : 363) discussed the small variations in colour and measurement found in this species. They considered that these were of a clinal nature and concluded that because of this it would be inadvisable to distinguish their birds from the Central Highlands as a separate race, although they differed somewhat from other populations. The material I have examined supports this conclusion, the underparts of the birds from the Central Highlands being, on the whole, rather more ashy in tone when compared with other populations. This difference however, is not constant and there is some individual variation for two adult males from Tomba match birds from the south-east. Although I have few adult males for comparison their measurements do not differ significantly from those of the birds from the Central Highlands.

MEASUREMENTS OF ADULT MALES OF *Amblyornis macgregoriae*

	Wing.	Tail.	Crest.
macgregoriae Owen Stanley Range (2)	132, 140	80	57, 61
aedificans Upper Waria River (2)	132, 138	80, 81	60, 61

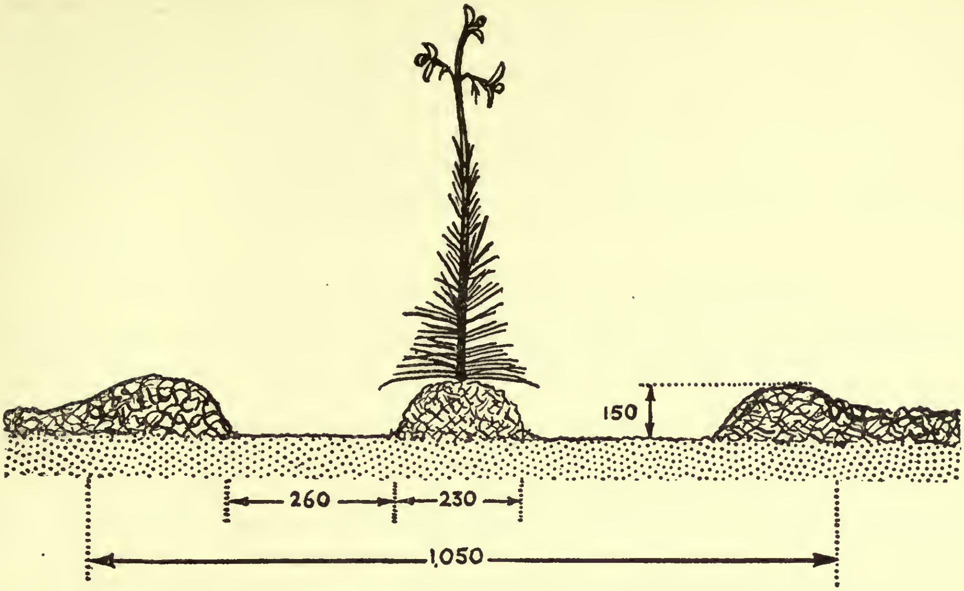

FIG. 2.—Sketch of a cross-section of the bower of *Amblyornis macgregoriae*. Measurements in millimetres. (*After Loke Wan Tho.*)

FIELD NOTE. Bowers were found on several coccasions; they were roughly circular in plan, but the dancing ground invariably formed a perfect circle. Each bower was built around a central sapling of *Garcenia* which the natives call "Kichan". One bower found deep in the moss forest was built of a dark moss and the playground was devoid of leaves.

Chlamydera lauterbachi lauterbachi Reichenow

Chlamydera lauterbachi Reichenow, 1897, Ornith. Monatsber. **5**, p. 24. Jagei River, upper Ramu River, Central Highlands, New Guinea.

1953.17.228–230; 1 ♂, 2 ♀; Minj, Wahgi River, 5,000 ft.; November, 1951.

MEASUREMENTS: 1 ♂—wing, 133; tail, 104; bill, 22. 2 ♀—wing, 126, 129; tail, 102, 103·5; bill, 22. COLOURS: bill, black; legs, olive-green; iris, brown. STOMACH CONTENTS: fruits and berries.

"This bower-bird is found in lightly wooded country. It was plentiful on the plateau drained by the Wahgi River, where it frequented small patches of secondary forest and the shrub around the edges of fields. It was often seen flying low from one small group of trees to another. The birds were breeding in November and several nests were observed. The normal clutch size appeared to be one egg. The bower is roughly circular in shape and about two feet in diameter. Inside there are two main runways approximately parallel to each other with their openings converging on opposite sides of the bower, The walls are about one foot high and built of interlaced sticks. The runways, or ramps, incline upwards from the openings towards the middle of the bower where, at their highest, they are joined by a smaller transverse runway ; thus in plan they form an H. The transverse runway is about ten inches long with walls about eight inches high built of very small sticks and twigs. A small heap of blue-coloured stones was found in this transverse runway and more stones and a few dark blue fruits in the main ones." (F. S.-M.). The design and construction of the bower agrees with the description given by Marshall (1954).

Daphoenositta miranda kuboriensis Mayr and Gilliard

Daphoenositta miranda kuboriensis Mayr and Gilliard, 1952, Amer. Mus. Novit. No. **1577**, p. 5. Mount O-Mar, Kubor Mountains, Central Highlands, New Guinea.

1953.17.231–233 ; 1 ♂, 1 (?) imm. ♂, 1 ? ; Lamende Range, 10,000 ft.; May, 1951, MEASUREMENTS : 1 ♂—wing, 87 ; tail, 43 ; bill, 10·5. 1 (?) imm. ♂—wing, 81 ; tail, 42 ; bill, 9·0. 1 ?—wing, 82 ; tail, 40 ; bill, 10·0. COLOURS : bill, black ; legs, black (?, yellow) ; iris, cream ((?) imm. ♂, yellow). STOMACH CONTENTS : small insects.

From the description of this race it seems that the doubtfully sexed specimen may be a female as the feet and legs are yellow in colour, whereas they are dark green in an adult male. Its plumage is similar to that of other adults, so it is unlikely to be a young bird. The plumage is fairly fresh in all the birds and there is no sign of moult. The specimens were taken in the wet moss forest high on the Lamende Range.

Neositta papuensis alba Rand

Neositta papuensis alba Rand, 1940, Amer. Mus. Novit. No. **1072**, p. 10. 15 km. south-west of Bernhard Camp, Idenburg, River, northern New Guinea.

Neositta papuensis wahgiensis Gyldenstolpe, 1955, Ark. f. Zool. 8, p. 153. Nondugl, Wahgi Valley, Central Highlands, New Guinea.

1953.17.234–236 1 ♂, 2 juv. ♂ ; Mount Giluwe, 8,000 ft.; June 1951. MEASUREMENTS : 1 ♂—wing, 84 ; tail, 38 ; bill (from nostril), 10·0. 2 juv. ♂—wing, 76·5, 78·5 ; tail, 34, 40 ; bill (from nostril), 9, 11. COLOURS : bill, pale yellow with black tip ; legs, yellow ; iris, yellow. STOMACH CONTENTS : insects.

The adult male matches a topotypical male taken by Dr. Rand. It is characteristic of *alba* in having the head and neck pure white all round and the feathers of the breast and abdomen paler edged than in *papuensis*. The female of *alba* is unknown but Gyldenstolpe (1955 : 153) described a single female from Nondugl which he distinguished as *wahgiensis*. It seems probable that this female may represent the hitherto unknown female of *alba* because of the identity of the males from Mount Giluwe ; but this point cannot be settled until topotypical females of *alba* have been collected. Meanwhile, I propose that *wahgiensis* should be regarded as a synonym of *alba*.

Field note. Three birds were seen in a tree where they appeared to be hunting for insects. They worked their way up and along the branches searching carefully and at long length among the moss.

Myzomela adolphinae Salvadori

Myzomela adolphinae Salvadori, 1875, Ann. Mus. Civ. Genova, **7**, p. 946. Arfak Mountains north-western New Guinea.

Field note. A solitary bird. Two or three would usually be seen at intervals along the drive of the bungalow where we stayed at Nondugl. Each bird would perch on the top of one of the small trees of the casuarinas hedge.

Myzomela rosenbergii wahgiensis Gyldenstolpe

Myzomela rosenbergii wahgiensis Gyldenstolpe, 1955, Ark, f. Zool. **8**, p. 155. Weiga, Sepik-Wahgi Divide, Central Highlands, New Guinea (7,400 ft.).

Field note. Native name " Kaltentepal ". A fairly common bird often seen flying from tree to tree in small flocks of a dozen or so, and heard calling out most of the time. A nest was found about 10 ft. above the ground in a small bush growing in a swamp, it was built of roots and lined with finer rootlets. Two young birds were found there (24th September), these were a dark chestnut brown above and a lighter brown below with a pale brown patch under the chin. The wings were a dark chestnut brown with a darker barring and the flight feathers black in colour. The gape and the inside of the mouth were yellow and the eyes brown, the legs were grey in colour, but the backs of the legs and the feet were yellow. Only the female was observed to feed the young birds, no male was seen to go to the nest. The juveniles defaecated with considerable force so that the faeces were ejected clear of the nest.

Melipotes fumigatus Meyer

Melipotes fumigatus A. B. Meyer, 1886, Zeitschr. ges. Ornith. **3**, p. 22. Hufeisenbirge, south-eastern New Guinea.

1953.17.237–238 ; 1 ♂, 1 ♀ ; Hagen Range, 7,000 ft.; December, 1950 ; January, 1951.

Measurements : 1 ♂—wing, 124 ; tail, 108 ; bill, 21. 1 ♀—wing, 115 ; tail, 100 ; bill, 20. Colours : bill, black ; legs, grey-blue ; iris, dark brown ; skin of face, orange. Stomach contents : berries and fruits.

The specimens match the description of the large-sized birds reported from the same locality by Mayr and Gilliard (1954 : 366) who also described a smaller and somewhat darker bird from the neighbouring Wahgi-Divide. They did not distinguish the birds trinominally because they were of the opinion that the differences were due not to geographical but to local altitudinal variations. In not naming these specimens racially I am following their decision. Gyldenstolpe (1955 : 157) identified the smaller bird as *goliathi* Rothschild and Hartert.

FIELD NOTE. Native name, " Mongkulle ". Several nests were found slung from the forks at the ends of the branches of the trees. They were between 15 and 20 ft. above the ground and made of leaves lined with rootlets and covered on the outside with moss. One nest contained an egg on 23rd September which had a beige-pink ground colour and red-brown spots that were more numerous towards the broader end. Another nest contained one juvenile on 7th October ; this was fed by only one of the parents, the other remained nearby and called unceasingly with a plaintive squeaking, " Wheet-wheet-wheet ". The food given to the young appeared to be fruit, on two occasions plum-coloured fruit was clearly seen to be offered. The species was fairly common, the flight being somewhat similar to that of a bulbul. It is probable that the patch of bare skin around the eye changes colour. (Mayr and Gilliard, 1954 : 367, reported a change in colour of the skin of this area after a bird had hung upside down for a short time.—R. W. S.)

Melidectes fuscus fuscus (De Vis)

Acanthochoera fusca De Vis, 1897, Ibis, Ser. 7, **3**, p. 383. Mount Scratchley, south-eastern New Guinea.

1953.17.239 ; 1 ♂ ; Hagen Range, 10,000 ft.; February, 1951.

1953.17.240–242 ; 1 ♂, 1 juv. ♂, 1 ♀ ; Mount Giluwe, 11,000–10,000 ft., April, May, 1951.

1953.17.243 ; 1 ♀ ; Lamende Range, 10,000 ft., May, 1951.

MEASUREMENTS : 2 ♂—wing, 108, 110 ; tail, 109, 110 ; total culmen, 29 ; tarsus, 33, 34. 1 juv. ♂—wing, 96 ; tail, 99 ; total culmen, 27 ; tarsus, 29. 2 ♀—wing, 95, 99 ; tail, 96, 100 ; total culmen, 28 ; tarsus, 31, 33. COLOURS : bill, black ; legs—2 ♂, pale blue-grey—1 juv. ♂, dark horn—2 ♀, dark grey ; iris, dark brown ; skin posterior to eye, brick red ; eye-wattle, pale blue (in juv. ♂ both skin posterior to eye and the eye-wattle are pale yellow). STOMACH CONTENTS : insects.

Mayr and Gilliard (1954 : 367) showed that the birds of this species in the Wahgi region are intermediate between the nominate form from south-eastern New Guinea and *occidentalis* from the Oranje and Nassau Ranges, the latter being separated on its smaller size. One female (May) taken on a nest containing a young bird is in worn plumage. The February and April birds are in moult, while the only May male is in fresh plumage.

FIELD NOTE. Native name, " Orboöi ". A nest containing one juvenile was found in the forest on 8th October. It was built of fine rootlets and lined with the red fibres of the frond of the tree-fern, the outside was decorated with moss. The juvenile was black in colour except for a blue-grey area of bare skin around the eye and other patches of bare skin near the ear and on the neck. The bill was black, the gape yellow and the tongue was brush-like—the same as the tongue of the adult bird. The legs were a blue-flesh colour. Both parents fed the young bird, unlike the adults of *M. belfordi* and *Melipotes fumigatus*, where only one of the parents did so. Unlike the former they were very tame and the adults continued to feed the juvenile while the observer was nearby. The food that was presented to the young bird consisted of insects and probably some nectar. The female was recognizable ; her wattles were very small and barely perceptible.

Melidectes princeps Mayr and Gilliard

Melidectes princeps Mayr and Gilliard, 1951, Amer. Mus. Novit. No. **1524**, p. 13. Mount Wilhelm, Bismarck Mountains, Central highlands, New Guinea.

1953.17.244 ; ? ; Minj River, Kubor Range, 9,000 ft.; October, 1950.

1953.17.245 ; ? ; Hagen Range, 10,000 ft.; January, 1951.

MEASUREMENTS : 2 ?—wing, 112, 113 ; tail, 105, 106 ; bill, 42, 44. COLOURS : bill, black ; legs, pale grey to blue ; iris, dark brown ; skin posterior to eye, bright yellow ; wattle cream.

These are probably adult females. They appear to be too small to be males (adult male : wing, 117–123 mm.) and are probably not young birds because the bearded parts of the chin and throat are white in colour, whereas this area is a yellowish-white in immature birds—Mayr and Gilliard (1954 : 13).

Melidectes belfordi (De Vis)

Melirrhophetes belfordi De Vis, 1890, Ann. Rep. Brit. New Guinea, **1888–89**, p. 60. Mount Knutsford, south-eastern New Guinea.

1953.17.246–248 ; 3 ♂ ; Hagen Range, 7,500 ft.; December, 1950 ; January, 1951.

1953.17.249–250 ; 2 ♂ ; Mount Giluwe, 7,800–7,500 ft.; April, 1951.

MEASUREMENTS : 3 ♂—(Nos. 1953.17.246, 247, 250) wing, 144–153 ; tail, 120–126 ; bill, 40–42. 2 ♂—(Nos. 1953.17.248, 249) wing, 138, 139 ; tail, 110, 112 ; bill, 40, 42. COLOURS : 3 ♂ (Nos. 1953.17.246, 247, 250)—bill, black ; legs, olive ; iris, dark brown ; skin around eye, pale blue. 2 ♂ (Nos. 1953.17.248, 249)—bill, pale blue-grey ; legs, pale blue-grey ; iris, dark brown ; gape-wattle, cream ; throat-wattle, brick red ; skin around eye, pale green-blue. STOMACH CONTENTS : berries, small insects and spiders.

The series consists of birds which differ markedly in appearance ; namely, " black-bills " (*belfordi*) and " wattle-birds " (*rufocrissalis*). These differences are so distinct that in the past *belfordi* and *rufocrissalis* were placed in different genera—*Melidectes* and *Melirrhophetes* respectively—and until recently were regarded as members of a super-species ; however, Mayr and Gilliard (1952*c*) concluded that they were conspecific. The two forms are allopatric and generally the " black-bills " replace the " wattle-birds " above a critical altitude of 2,000 to 2,500 metres, where hybrids are found grading between the two phenotypes. The present series was taken near the critical hybridization altitude and each bird exhibits some degree of heterogeneity. By adopting the scoring system used by Mayr and Gilliard (1952*c*) to indicate the degree of hybridization it is possible to show how much the individual specimens differ from the phenotypes. Assuming that a true " black-bill " scores 0 and a true " wattle-bird " 100, the birds before me score as follows :—

1953.17.246	3
1953.17.247	11
1953.17.250	22
1953.17.248	60
1953.17.249	89

Generally Nos. 246, 247, 250 could be regarded as " black-bills " and the other two specimens, Nos. 248 and 249, as " wattle-birds ".

FIELD NOTE. Native name, " Arglua ". Several nests were found built from 8 to 15 ft. above the ground in the slender forks towards the end of the branches. They looked like woven baskets of fine grasses and fern stalks, covered and suspended by moss. One nest, first examined on 4th October, was kept under observation ; it contained only one juvenile. The young bird had a black head with a fringe of sandy coloured down around the crown and a lighter coloured patch around each eye. The upper-parts were dark grey and the under-parts somewhat lighter in colour, with white streaks on each side of the chin ; the under-tail coverts were cinnamon. The bill was mainly grey in colour with some white on it. Both of the parents fed the young bird, but one did so less frequently than the other and usually remained close by the nest. The food appeared to consist mainly of insects ; but it is probable the nectar was given also because sometimes one of the adults would return to the nest and stand over the juvenile and rapidly flick its long reddish tongue in and out of the young bird's mouth. When neither of the adults could be seen they could still be heard nearby making clucking noises ; generally they were very noisy. One loud call that they made frequently was one of the common calls of the forest. Their alarm call could not be established with certainty, but it appeared to be either, " Quick-quick-quick-quick, kiow-kiow-kiow-kiow ", or, " tolle-tolle-tolle, kiow-kiow-kiow-kiow " ; in response to this call the young bird would freeze in the middle of the nest and close its eyes. They were very shy birds and easily disturbed.

Oreornis subfrenatus salvadorii (Hartert)

Ptilotis salvadori Hartert, 1896, Novit, Zool. **3**, p. 531. Owen Stanley Mountains, south-eastern New Guinea.

1953.17.251 ; 1 ♂ ; Mount Giluwe, 7,800 ft.; April, 1951.

MEASUREMENTS : 1 ♂—wing, 105 ; tail, 95 ; bill, 21. COLOURS : bill, black (gape, yellow) ; legs, blackish yellow ; iris, dark brown ; bare skin behind eye, bright yellow. STOMACH CONTENTS : small insects.

Nearest to *salvadorii* but slightly lighter in colour ; it differs from *melanolaema* in being darker—the under-parts being less brownish and more greyish olive in colour. I am indebted to Professor Stresemann, who kindly compared the bird with material of the latter in the Berlin Museum.

Ptiloprora guisei umbrosa Mayr

Ptiloprora guisei umbrosa Mayr, 1931, Mitt. Zool. Mus. Berlin, **17**, p. 666. Schraderberg (2,000 ft.), Sepik Mountains, Central Highlands, New Guinea.

1953.17.252–253 ; 2 ♂ ; Mount Giluwe, 7,500 ft.; June, 1951.

MEASUREMENTS : 2 ad. ♂—wing, 88, 91 ; tail, 76 ; bill, 21, 22. COLOURS : bill, black ; legs, grey-blue ; iris, latteine green. STOMACH CONTENTS : small insects.

FIELD NOTE. Native name, " Tongklà ". A nest was found suspended on a living vine of *Hoya*. It was built of rootlets and dried leaves of the climbing bamboo and lined with the hairs from a tree-fern. The outside of the nest was decorated with living moss apart from one part that was covered by a broad leaf of the vine. The adult often held its tail high like a pipit as it jumped from branch to branch, sometimes it would dive to the ground in pursuit of insects and carry them to the nest. There were young in the nest on 10th October and both parents shared in rearing them ; the parents fed the young by clinging upside down to the vine. The call was a clear whistle, " Choo-weei-oo ", but as they approached the nest the adults made a "chucking" sound.

Paramythia montium montium De Vis

Paramythia montium De Vis, 1892, Ann. Rep. Brit. New Guinea, **1890–91**, p. 95. Mount Suckling, south-eastern New Guinea.

1953.17.267, 270–271 ; 1 ♂, 2 ♀ ; Mount Giluwe, 9,500–9,000 ft.; March, 1951.

1953.17.268–269 ; 1 juv. ♂, 1 ♀ ; Hagen Range, 9,500 ft.; January, February, 1951.

MEASUREMENTS : 1 ♂—wing, 106 ; tail, 100 ; bill, 16. 1 juv. ♂—wing, 102 ; tail, 95 ; bill, 15. 3 ♀—wing, 105–106 ; tail, 89–98 ; bill, 15–16. COLOURS : bill, black ; legs, black ; feet, black. STOMACH CONTENTS : fruits and berries.

FIELD NOTE. Native name, " Kai-ingkun ".

Zosterops novaeguineae wahgiensis Mayr and Gilliard

Zosterops novaeguineae wahgiensis Mayr and Gilliard, 1951, Amer. Mus. Novit. No. **1524**, p. 14. Nondugl, Wahgi Valley, Central Highlands.

1953.17.254 ; 1 ♂ ; Wahgi River ; 5,200 ft.; November, 1951.

MEASUREMENTS : 1 ♂—wing, 62·5 ; tail, 42·5 ; bill, 11. COLOURS : bill, dark horn paler at base ; legs, grey ; iris, yellow-brown. STOMACH CONTENTS : berries.

FIELD NOTE. A flock of about 15 to 20 of these small birds was seen near the camp at Tomba.

Erythrura trichroa sigillifera (De Vis)

Lobospingus sigillifer De Vis, 1897, Ibis, Ser. 7, **3**, p. 389. Mountains of south-eastern New Guinea, apparently Mount Scratchley.

1953.17.255, 257; 1 ♂, 1 juv. ♀; Hagen Range, 7,500 ft.; December, 1950; January, 1951.

1953.17.256 1 ♂ Mount Giluwe 8,500 ft.; May, 1951.

MEASUREMENTS: 2 ♂—wing, 60, 61; tail, 44; bill, 12. 1 juv. ♀—wing, 58; tail, 39; bill, 11. COLOURS: bill, black; legs, pale horn; iris, brown-black. STOMACH CONTENTS: small berries and seeds.

Lonchura spectabilis wahgiensis Mayr and Gilliard

Lonchura spectabilis wahgiensis Mayr and Gilliard, 1952, Amer. Mus. Novit. No. **1577**, p. 7 Kegalsugl, Mount Wilhelm, Bismarck Mountains, Central Highlands, New Guinea; 8,000 ft.

1953.17.258; 1 ♀; Minj, Wahgi River, 5,000 ft.; November, 1950.

MEASUREMENTS: 1 ♀—wing, 49; tail, 32; bill, 10·5. COLOURS: bill, blue-grey; legs, dark blue-grey; iris, black. STOMACH CONTENTS: grass seeds.

Seen in large flocks on the grasslands. This specimen was taken on a nest containing four eggs.

Oreostruthus fuliginosus hagenensis Mayr and Gilliard

Oreostruthus fuliginosus hagenensis Mayr and Gilliard, 1954, Bull. Amer. Mus. Nat. Hist. **103**, p. 372. Mount Hagen, Central Highlands, New Guinea.

1953.17.259–265; 4 ♂, 3 imm. ♂; Mount Giluwe, 11,500–9,000 ft.; April, May, June, 1951.

MEASUREMENTS: 4 ♂—wing, 67–68; tail, 44; bill, 9·5–10. 3 imm. ♂—wing, 66–68; tail, 40–44; bill, 8·5–9·5. COLOURS: 4 ♂—bill, coral red; legs, brown-horn; iris, orange-red. 3 imm. ♂—bill, black (gape, yellow); legs, brown-horn; iris, brown. STOMACH CONTENTS: grass seeds.

This race was separated on two specimens from Mount Hagen which differed, among other characters, from *fuliginosus* De Vis and *pallidus* Rand in the back being thinly diffused with blood-red markings. Now more material is available it seems that this character is not constant, for only one adult male in this series has any red on the back and then it is seen as a wash which is restricted to a small area. In other respects these birds match the description of *hagenensis*. The immature birds differ from the adults in the under-parts not being marked with blood-red. In comparison with *fuliginosus* the immature birds are darker above and lighter below. The adults are completing moult and the testes are enlarged. This fine series was taken on the mid-mountain and alpine grasslands of Mount Giluwe.

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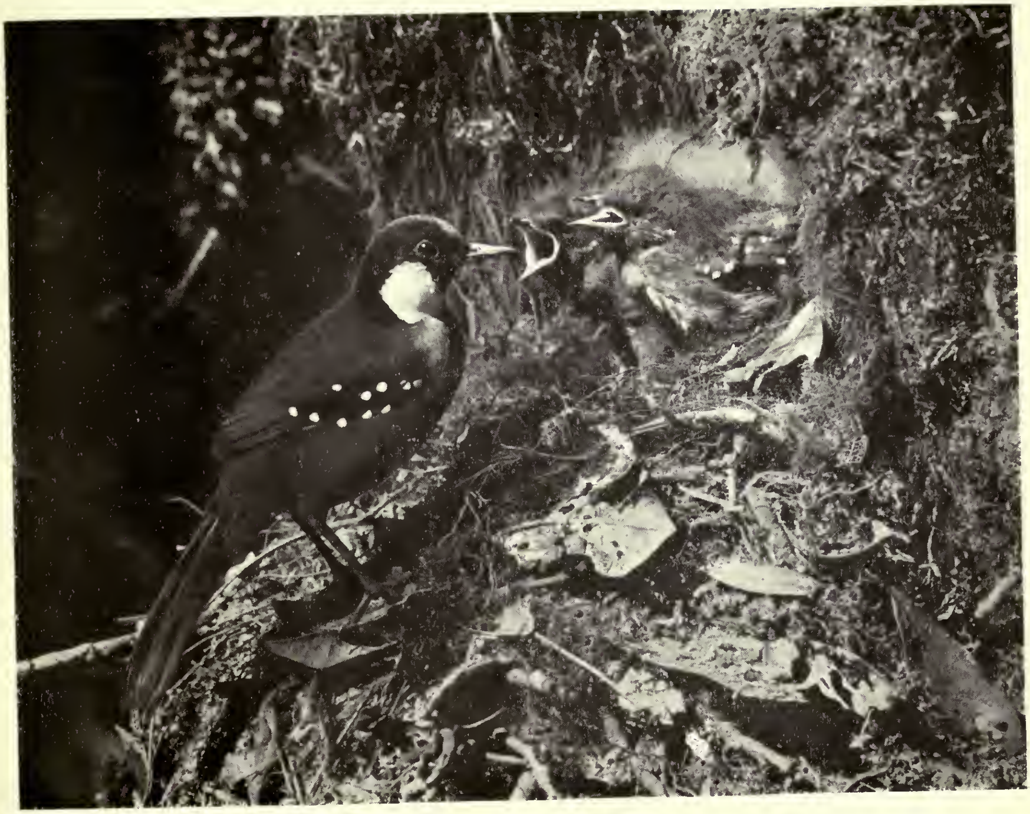
PLATE 13.

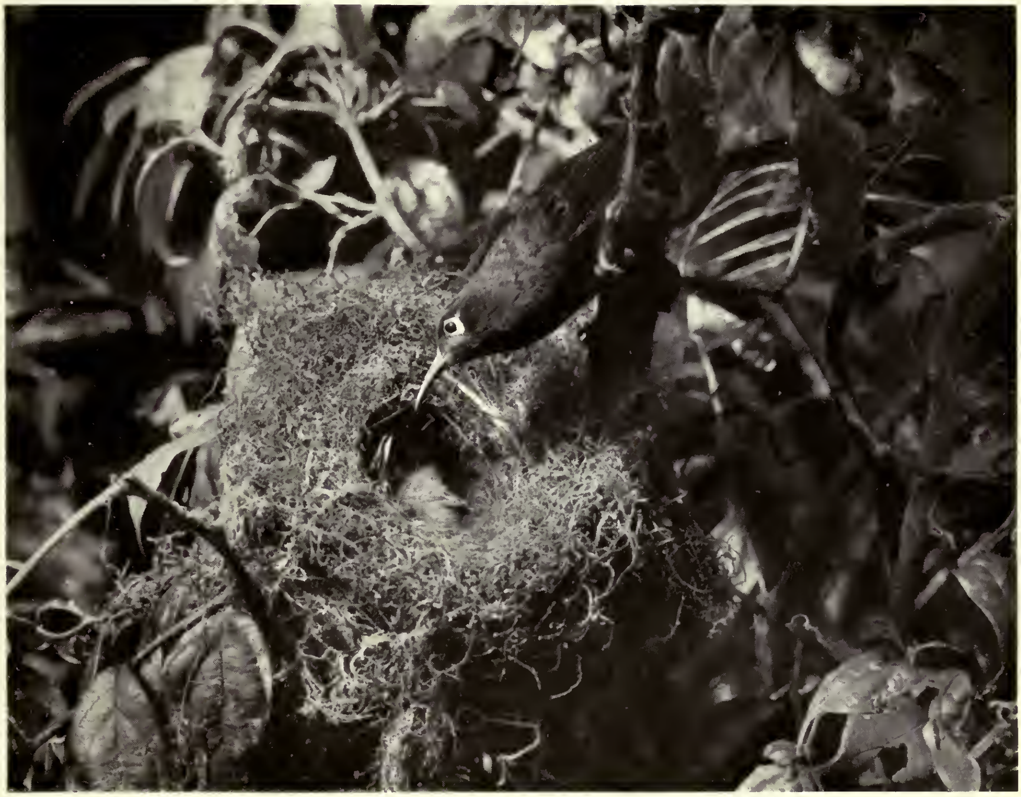
Eupetes leucostictus. Adult, nest and nestlings. Wahgi region, Central Highlands, New Guinea, 8,000 ft. October 5th, 1952. *Photo : Loke Wan Tho.*



EUPETES LEUCOSTICTUS.

PLATE 14.

Melidectes fuscus. Adult, nest and nestling. Tomba, Hagen Range, Central Highlands, New Guinea ; 8,000 ft. October 9th, 1952. *Photo : Loke Wan Tho.*



MELIDECTES FUSCUS.

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